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2nd International Workshop of Malacology

Systematics, Phylogeny and Biology of Opisthobranchs Molluscs

Istituzione Culturale Federico II

Menfi, 10-14 June 1999

(Juan Lucas Cervera & Riccardo Cattaneo Vietti, eds)

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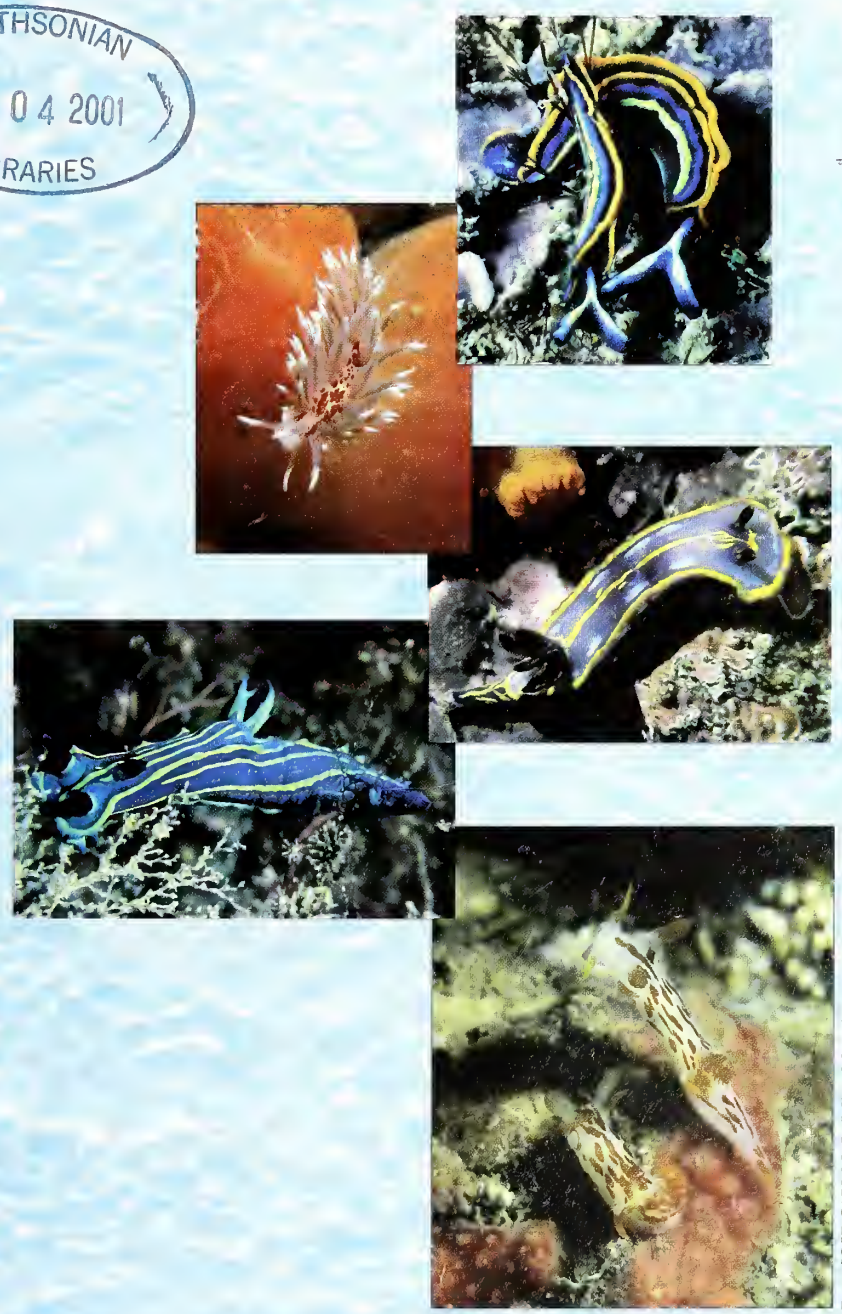

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Nando, ottanta anni

Sembra facile. Sembra.
Quando con Rikkardo abbiamo pensato a questo omaggio al "fondatore' in occasione dei suoi 80 anni (ciò avverrà, o sarà avvenuto, il 15 agosto 2001) sembrava ancor più facile, facilissimo. Il classico 'buttar giù due righe' e via.
Ora, con la pagina bianca davanti sono alcuni giorni che rimando e navigo mentalmente tra gli splendidi (e si, lo sono) 'concetti spaziali' di Lucio Fontana ed i 12 (o più, dipende dalle edizioni) volumi della vita di Casanova.
Perché hai un bel da dire ma Nando (Il Dr. Fernando Ghisotti, il Presidente) pur non assomigliandomi in alcun modo, in una o due paginette ci sta stretto. Molto stretto.
Poiché é statisticamente noto, affermato e conclamato che i malacologi sono, sono stati e, vivaiddio, saranno, tutti longevi centenari, ad altri certamente toccherà attorno al 2020/2030 il compito di elogiare, elencare, ricordare le molte cose fatte dal Nostro.
Io proverò ora semplicemente a raccontare a tutti voi, ciò che tutti voi già ben sapete.
Ad esempio la sua sontuosa gentilezza e disponibilità a perdere tempo con tutti e per tutti. La profonda conoscenza di tutto (o quasi) sempre trincerandosi dietro cauti 'mi

pare', 'credo', 'forse é così'. L'energico decisionismo soavemente ammantato da spiegazioni (a posteriori, sempre) disarmanti per il candore e la logica inoppugnabile. Sempre.
La signorilità, sempre, comunque, ovunque, con chiunque. E dico chiunque ...
L'ironia, la passione per i calembour, per i giochi di parole, infantili (in apparenza almeno) per le battute, indimenticabili così come le sue lettere.
Veramente si può dire che nella forma scritta Nando ha fatto rifulgere il meglio di sé. Delicatamente sfarfallando dall'argomento serio oggetto della missiva, a divagazioni, doppi sensi, citazioni dotte volgarizzate all'uopo con garbo crudele e chiusure sempre esilaranti.
Oltre alle tante cose che, nella mia vita, so di dovergli per ciò che mi ha insegnato, ho avuto la fortuna di averne non poche di lettere sue e ciò mi é, anche, servito moltissimo nel mantenere alta la stima attorno a me; perché sia in casa che in ufficio quando mi si vedeva ridere da solo con un foglio in mano in luogo di pensare a più o meno precoci degenerazioni cerebrali sentivo sempre dire : "una lettera del Dr. Ghisotti, vero?"
Come vecchio amico, avrei davvero voluto raccogliere ripescando tra gli 'amici di penna' un collage di tutti i 'nonsense', delle battutine, delle frasette ingenue, dei giochini di Nando per farne un'edizione sul tipo di quella che la (altrettanto spiritosa) moglie Lisette (al secolo signora Elisabetta Steinmann in Ghisotti, di non celata stirpe schvizzzera) gli dedicò per i 60 anni. Il titolo, di origini solo apparentemente erudite, era 'Homo ludens' ed il serissimo, assolutamente sempre composto e misurato, coltissimo, distintissimo ed etereo Nando questo é, in fondo. Beato lui (e fortunati i suoi amici).
Parlando di Lisette mi é impossibile non citare la frase che sempre, quando qualcuno in qualche modo elogia il suo (anche per lei, ovviamente) incomparabile consorte lei profferisce con vera indignazione "Si, però 'Nando nnonn é buono. Nnonn é affatto buono!"
Come poi a questo punto dimenticare le accoppiate malacologico/umane Urio/Nando dapprima, col nostro seriosissimo e rigoroso contabile che sembrava il suo esatto opposto sotto tutti i sensi; ma sotto, di poco sotto, il mitico Rag. Urio era un personaggio ironico col quale potevi scherzare di tutto e su tutto; tranne naturalmente due cose : ritardare anche di una sola settimana il pagamento delle quote sociali e parlar male di D'Annunzio.
E la seconda accoppiata Nando/Giorgio Barletta, quella del definitivo salto di qualità scientifico associativo. Difficile non ricordare con immenso affetto e nostalgia, i silenzi eloquentissimi, gli occhi parlanti di Giorgio, la sua grande qualità nel non apparire mai essendoci sempre.
Che coppie, altri tempi davvero.
Altre coppie però, mi sia consentito ancora di ricordare (che Nando monogamo si, ma misogino mai) : i 'duetti' di Nando con Giulio Melone per raccontarsi la stessa barzelletta per la decima volta e con l'aria seria di due cattedratici di un tempo che si scambiano

risultati di ricerche profonde, e fingendo entrambi di non ricordare nulla.O simposi gastronomici nel cremasco, ove le affinità della padrona di casa, Andreana, col Nostro sono sempre apparse a tutti assai simili a tutte quelle sopra citate.Un completamento, una complicità, una perfetta liason, un idemsentire nel quale Nando era/é uno bino e trino, ma semper lù, come direbbe (spero) il suo amatissmo Carlo Porta.

Volgendo queste righe alla fine (ed alla malacologia in fine) voglio solamente ricordare che fin dai suoi esordi Nando mostrò una capacità imprenditoriale che sempre ha tenuto d'occhio la solidità economica ed unendovi le eccezionali qualità di concretezza e serietà scientifica fece della SIM (UMI, SMI) dapprima una realtà viva, attiva, ove convivevano malacologi ufficiali e collezionisti più o meno incolti. Senza superbia gli uni e senza modestia gli altri : assieme per merito di questo mixage la malacologia italiana della seconda metà del secolo scorso questo é stato e poco più. Quella mediterranea poi senza dubbio alcuno é per merito di quel gruppo da lui guidato che é risorta (o forse e non paia poi affermazione così sciovinistica, é nata).

Carissimo Nando, ci ho messo molte righe e ti rubo una battuta ("Non trovo mai il tempo per essere conciso") ma quello che volevo dirti io a nome di tutti gli amici malacologi é semplicemente : 'Auguri, auguri e molte volte grazie

Piero Piani

Questo importante volume é stato dedicato a Ferdinando Ghisotti, presidente onorario e socio fondatore della SIM, in occasione del suo ottantesimo compleanno grazie alle sponsorizzazioni degli amici che hanno parzialmente coperto le maggiori spese di stampa.

Libreria Naturalistica
Piero Piani

Riccardo Giannuzzi Savelli
Francesco Pusateri

Maria Antonietta Fontana

Adriana Castelli, Alberto Cecalupo, Giulio Melone, Gianni Sartore

Presentazione

Il Comune di Menfi possiede, grazie alla generosa donazione dell'esperta studiosa di Malacologia Vanna Rotolo Lombardo, una collezione di conchiglie di oltre 6000 esemplari, provenienti dal Mare di Porto Palo di Menfi e da tutti i Mari della Terra; un patrimonio di cultura naturalistica eccezionale, sapientemente tesaurizzato e coordinato in una Mostra Permanente, appositamente realizzata dall'Istituzione Culturale "Federico II" di Menfi, nei locali della Biblioteca Comunale.

Una raccolta di gioielli della natura, stupefacente, sempre più valorizzata e conosciuta tramite l'organizzazione di un Workshop Internazionale di Malacologia voluto dall'Istituzione Culturale Menfitana, con cadenza annuale, affinché la collezione non diventi un freddo espositore di "specie", ma un centro pulsante di studi e ricerca di cultura naturalistica nella Società e nella Scuola.

Al 2° Workshop Internazionale di Malacologia (intitolato: "*Sistematica, Filogenesi e Biologia dei Molluschi Opistobranchi*") tenutosi a Menfi nei locali dell'Auditorium della Biblioteca Comunale dal 10 al 14 Giugno 1999, hanno partecipato Esperti, Studiosi e Ricercatori di Malacologia che hanno trattato il tema proposto con interessanti relazioni scientifiche.

Tali contributi, pubblicati in questo volume, redatti con zelo e precisione scientifica, grazie alla divulgazione voluta dalla Società Italiana di Malacologia e patrocinata dall'Istituzione Culturale "Federico II", diventano così Atti che contribuiscono a dare al mondo scientifico nuovi risultati inerenti gli Opistobranchi.

Questi ultimi sono i Molluschi marini con il più elevato numero di specie che rivestono un ruolo ecologicamente importante: essi rappresentano, per la biologia marina, degli indicatori biologici, essendo animali estremamente delicati, dal breve ciclo vitale, che preferiscono vivere in acque incontaminate.

Il 2° Workshop Internazionale di Malacologia, considerato dal mondo accademico come "l'avvenimento scientifico mondiale del 1999", ha portato Menfi ad assurgere a "Capitale" internazionale della Malacologia, trasformandola in un pregnante Centro di irradiazione culturale naturalistica per sempre più preservare le misteriose meraviglie del pianeta blu, delle quali gli anfratti marini sono i gelosi custodi.

Gioacchino Mistretta

Vice presidente Istituzione Culturale "Federico II" - Menfi

Foreward

The papers presented in this issue of the Bollettino Malacologico stem from the 2nd International Workshop of Malacology under the specific topic "Systematic, Phylogeny and Biology of Opisthobranch Molluscs", held in Menfi (Sicily), in June 1999.

A few years ago, the Società Italiana di Malacologia and the Istituzione Culturale Federico II of Menfi, with the support of the Menfi Municipality and the Cantine Settesoli, undertook the commendable step of organising a series of annual meetings or international workshops, each one on a concrete theme within the wide scope of malacologia. This initiative has allowed a several groups of experts on specific research fields to meet during few days in a scenic village along the Sicilian coast.

So far, three of these workshops have been held. The first was entitled: "La Conservazione della Natura e dei Molluschi" (June 1998), the second is the subject of this volume, and the last, under the topic "Systematics, Phylogeny and Biology of Neogastropoda‰ was organised on June 2000. A fourth symposium will be held in June 2001 on "Systematics, Phylogeny and Biology of Polyplacophora".

The volume 36 (1-4) of the Bollettino Malacologico included some of the papers presented at the first of these symposia. The present issue contains some of the forty oral and poster contributions presented at the second symposium, focused on opisthobranch gastropods, including three of the invited lectures. The Scientific Committee of this meeting was constituted by Juan Lucas Cervera and Renato Chemello, and Vanna Rotolo was the administrative organiser. It was their great effort that made this outstanding event possible.

This meeting united about forty researchers from ten different countries, five of which were invited to address plenary lectures: Kathe Jensen, Christopher Todd, Bill Rudman, Guido Cimino and Terrence Gosliner. The sessions were divided into the following four topics: 1) Systematic and Phylogeny, 2) Ecology and Behaviour, 3) Biogeography, and 4) Biochemistry and Physiology.

Unfortunately, and due to several reasons, not all the presented papers could be included in the present volume. A dozen articles have been published finally here, focused mainly on Taxonomy-Systematics and Biology-Ecology. Most of them deal with the always popular nudibranchs, two with cephalaspids, and one with sacoglossans.

Although it is not possible to define a major theme in the workshop, this collection of papers represents an overview of the current work on opisthobranchs. It covers a variety of different aspects in the study of this fascinating group of animals. However, there are, evidently, significant gaps in the coverage of the groups and research fields.

The first three articles are invited lectures. Christopher Todd and collaborators provide a stimulating critical overview of some of the topics on the biology and ecology of nudibranch molluscs, like stenophagy, life cycles and life history, egg sizes, simultaneous hermaphroditism or poecilogony. Kathe Jensen's paper is a comparative review of the functional morphology of reproductive systems in the Sacoglossa. She gathers data from 98 species that are summarised and their phylogenetic and evolutionary importance discussed. Terrence Gosliner deals with the evolution of aposematic coloration and mimicry in opisthobranch molluscs within a phylogenetic framework.

There is also a group of six papers dealing primarily with taxonomy. Shireen Fahey and Terrence Gosliner review the genus Halgerda *in Western Australia and describe four new species. Michael Schrödl studies the South American opisthobranchs collected by Charles Darwin during the "Beagle" expedition, identifying some of Darwin's Magellanic opisthobranchs to the species level. Rebecca Johnson and Terrence Gosliner describe two new species of the genus* Thorunna *from the tropic Indo-Pacific. In the paper of Claudia Muniain, the dorid* Geitodoris patagonica *is redescribed, and she also draws attention to its defensive behaviour, comparing the mechanical and chemical strategies found in other Magellanic dorid nudibranchs. Marco Oliverio and Lionello Tringali present two papers, one of them reviewing the cephalaspid genus* Pyrunculus *in the Mediterranean, and the other dealing with the types of opisthobranch species described by Monterosato with a discussion on their identity.*

Another two papers are specifically focused on aspects of feeding behaviour and food sources. One of them, by Calado and Urgorri, on Calma glaucoides, *and the other by Cattaneo-Vietti and collaborators on* Discodoris atromaculata. *Finally, a single paper, presented by Gilianne Brodie, is essentially a comparative histological study of the radulaless dorid genera* Doriopsilla *and* Dendrodoris *(Porostomata, Dendrodorididae), that searches for new character sets to address their phylogenetic placement within this difficult group of nudibranchs.*

This is not the first time that a collection of papers focusing exclusively on opisthobranch molluscs have been presented and published in a malacological journal. The first precedent was the volume 5 number 2 of the American Malacological Bulletin (1987), which included some papers under the title "Symposium on the Biology and Evolution of opisthobranch molluscs". There also two precedents in this same journal: the volumes 24 (9-12) and 29 (5-8) of the Bollettino Malacologico, the first dedicated to the memory of Giorgio Barletta, deceased on February 1988, while the second collected the papers presented in the "Workshop on Systematics and Ecology in the Opisthobranch" organised during the 11th International Malacological Congress in Siena (1992). In 1991, both the Journal of Molluscan Studies (volume 57, part 4, supplement) and Malacologia (volume 32, no. 2) published monographic issues on Opisthobranchs. The former entitled "T.E. Thompson Memorial Issue", and the latter including many communications presented to the symposium "Evolutionary biology of Opisthobranchs" that took place during the 9th International Malacological Congress, held in Edinburgh (summer 1986).

The present issue constitutes a new collection of papers on opisthobranchs, a new step forward in the knowledge of this group of molluscs, and a good opportunity to review the state of the art research of this field.

I am sure that the efforts of the Scientific Committee of this workshop, the local organizing committee and institutions, the editors, authors, and reviewers, whose comments improved the manuscrips, have been well invested in this interesting volume.

José Templado
Museo Nacional de Ciencias Naturales
Madrid, 30-03-2001

Prefazione

Gli articoli inclusi nel presente volume sono stati presentati al secondo International Workshop of Malacology dal tema: "Sistematica, Filogenesi e Biologia dei molluschi opisthobranchi", tenuto a Menfi (AG, Sicilia), nel giugno 1999.

Alcuni anni orsono la Società Italiana di Malacologia e l'Istituzione Culturale Federico II di Menfi, col supporto del Comune di Menfi e delle Cantine Settosoli, iniziarono il lodevole lavoro di organizzare una serie di incontri annuali (international workshop), ciascuno dedicato ad uno specifico e concreto tema malacologico. Tale iniziativa ha permesso a vari gruppi di esperti in specifici settori di ricerca di incontrarsi per alcuni giorni tra i piacevoli scenari delle coste siciliane.

Finora tre workshop sono stati tenuti. Il primo fu dedicato a: "La Conservazione della Natura e dei Molluschi" (giugno 1998). Il secondo è il soggetto di questo volume. Il terzo fu organizzato nel giugno 2000 su: "Sistematica, Filogenesi e Biologia dei Neogastropoda". Un quarto incontro si terrà nel giugno 2001 su "Sistematica, Filogenesi e Biologia dei Polyplacophora".

Il volume 36(1-4) del Bollettino Malacologico ha incluso alcuni degli articoli relativi ai lavori presentati nel primo workshop. Questo volume contiene una parte dei quaranta contributi (orali e a poster) presentati al secondo simposio, centrati sui gasteropodi opistobranchi, incluse tre relazioni ad invito. Il Comitato Scientifico del convegno era costituito da Juan Lucas Cervera e Renato Chemello, mentre Vanna Rotolo lavorò come organizzatrice logistica. È stato grazie al loro grande sforzo cooperativo che questo evento è stato possibile.

Questo incontro ha unito una quarantina di scienziati da dieci diversi paesi, cinque dei quali furono invitati a presentare comunicazioni generali introduttive: Kathe Jensen, Christopher Todd, Bill Rudman, Guido Cimino e Terrence Gosliner. Le sessioni furono divise a seconda dei seguenti temi: 1) Sistematica e Filogenesi, 2) Ecologia e Comportamento, 3) Biogeografia, e 4) Biochimica e Fisiologia.

Sfortunatamente, a causa di varie ragioni, non tutti i lavori presentati hanno potuto essere inclusi nel presente volume. Una dozzina di articoli sono finalmente qui pubblicati, principalmente centrati su Tassonomia-Sistematica e su Biologia-Ecologia. Molti trattano dei sempre popolari nudibranchi, e uno dei sacoglossi.

Benché non sia possibile definire un tema guida dominante nel workshop, questa raccolta di lavori rappresenta uno sguardo d'insieme della ricerca attuale sugli opistobranchi.Vengono trattati i diversi aspetti dello studio di questi affascinanti animali, e ciononostante si rilevano delle lacune significative nel ventaglio delle tematiche e dei gruppi trattati.

I primi tre articoli sono relazioni ad invito. Christopher Todd e i suoi collaboratori danno una revisione critica dei vari temi della biologia e dell'ecologia dei nudibranchi, come la stenofagia, i cicli vitali e la storia naturale, le dimensioni delle uova, l'ermafroditismo simultaneo o la pecilogonia. Il lavoro di Kathe Jensen è una review comparativa della morfologia funzionale dei sistemi riproduttivi nei the functional morphology of reproductive systems in the Sacoglossa. L'Autrice ha raccolto dati da 98 specie, riassunti e sintetizzati nel loro significato filogenetico ed evolutivo. Terrence Gosliner tratta l'evoluzione dell'aposematismo e del mimetismo negli opistobranchi in un ambito filogenetico.

C'è quindi un gruppo di sei lavori che tratta primariamente la tassonomia. Shireen Fahey e Terrence Gosliner revisionano il genere Halgerda *in Australia occidentale e descrivono quattro nuove specie. Michael Schrödl studia gli opistobranchi sudamericani raccolti da Charles Darwin durante il viaggio sulla "Beagle", identificando alcune degli opistobranchi magellanici di Darwin a livello specifico. Rebecca Johnson e Terrence Gosliner descrivono due nuove specie di* Thorunna *dall'Indo-Pacifico tropicale. Claudia Muniain ridescrive il doride* Geitodoris patagonica, *e evidenzia il suo comportamento difensivo, comparando le strategie meccaniche e chimiche riscontrate in altri nudibranchi doridi magellanici. Marco Oliverio e Lionello Tringali presentano due lavori, uno di revisione del genere cefalaspideo* Pyrunculus *in Mediterraneo, e l'altro sui tipi delle specie di opistobranchi descritte da Monterosato con una discussione sulla loro identità.*

Altri due lavori sono dedicati specificatamente agli aspetti del comportamento alimentare e delle risorse trofiche. In uno Calado e Urgorri trattano Calma glaucoides, *mentre nell'altro Cattaneo-Vietti e collaboratori si occupano di* Discodoris atromaculata. *Infine l'articolo di Gilianne Brodie è essenzialmente un lavoro di istologia comparata dei generi privi di radula* Doriopsilla *e* Dendrodoris *(Porostomata, Dendrodoriddae), alla ricerca di nuovi set di caratteri per investigare le relazioni filogenetiche in questo difficile gruppo di nudibranchi.*

Non è questa la prima volta che un gruppo di lavori dedicati esclusivamente agli opistobranchi viene presentato e pubblicato il una rivista malacologica. Il primo precedente fu nel fascicolo 5 (2) dell'American Malacological Bulletin (1987), che incluse alcuni articoli sotto il titolo "Symposium on the Biology and Evolution of opisthobranch molluscs". Anche nello stesso Bollettino Malacologico ci sono altri due precedenti: i fascicoli 24 (9-12) e 29 (5-8), il primo dedicato alla memoria di Giorgio Barletta, deceduto nel Febbraio 1988, il secondo che raccoglie i lavori presentati nel "Workshop on Systematics and Ecology in the Opisthobranch" organizzato durante l'undicesimo International Malacological Congress, tenuto a in Siena (1992). Nel 1991, sia il Journal of Molluscan Studies 57(4), supplement, sia Malacologia 32(2) hanno pubblicato numeri monografici sugli opistobranchi. Il primo intitolato "T.E. Thompson Memorial Issue", e il secondo comprendente molte comunicazioni presentate al simposio "Evolutionary biology of Opisthobranchs" tenuto durante il nono International Malacological Congress (Edinburgh, 1986).

Questo fascicolo costituisce una nuova raccolta di lavori sugli opistobranchi, un nuovo passo in avanti nella conoscenza di questo gruppo di molluschi, ed una buona opportunità di dare uno sguardo d'insieme allo stato dell'arte nella ricerca in questo campo.

Sono sicuro che gli sforzi del Comitato Scientifico di questo workshop, degli organizzatori e delle istituzioni locali, degli editori, degli autori e dei revisori i cui commenti hanno migliorato i manoscritti, sono tutti stati ben investiti nella produzione di questo interessante volume.

José Templado
Museo Nacional de Ciencias Naturales
Madrid, 30-03-2001

On the genus *Halgerda* (Nudibranchia: Halgerdidae) from Western Australia with descriptions of four new species

Shireen J. Fahey, Terrence M. Gosliner

KEY WORDS: Phylogenetics, systematics, *Halgerda*, nudibranch, Western Australia, Indo-Pacific

ABSTRACT Four new species of *Halgerda* from Western Australia are named and described anatomically. These new species: *Halgerda gunnessi* sp. nov., *H. theobroma* sp. nov., *H. maricola* sp. nov. and *H. brycei* sp. nov. are more highly derived in several aspects of their morphology than other species of *Halgerda*. This brings to eight, the number of *Halgerda* species recorded from Western Australia. A specimen of *Halgerda formosa* Bergh, 1880, also collected in Western Australia, is examined and compared to specimens collected from the western Indian Ocean. Comparisons of the four new species are made with the original and subsequent descriptions of *Halgerda formosa* Bergh, 1880, *H. aurantiomaculata* Allan, 1932; *H. carlsoni* Rudman 1978; *H. malesso* Carlson & Hoff, 1993; *H. stricklandi* Fahey & Gosliner, 1999; *H. bacalusia* Fahey & Gosliner, 1999; *H. diaphana* Fahey & Gosliner, 1999b; *H. johnsonorum* Carlson & Hoff, 2000 and *H. batangas* Carlson & Hoff, 2000. The coloration, reproductive system and the radular morphology of the four new species differ significantly from previously described *Halgerda* species. Morphological and anatomical data from the new *Halgerda* species are used to refine the preliminary phylogeny of this genus. The phylogenetic analysis confirms the monophyly of *Halgerda* and its relationship to its outgroup *Asteronotus* Ehrenberg, 1831.

RIASSUNTO Quattro nuove specie di *Halgerda* dell'Australia occidentale vengono descritte: *Halgerda gunnessi* sp. nov., *H. theobroma* sp. nov., *H. maricola* sp. nov. e *H. brycei* sp. nov. Queste specie presentano diversi caratteri morfologici assai più derivati che in altre specie di *Halgerda*. Ciò porta ad otto il numero di specie di *Halgerda*, conosciute per l'Australia occidentale. Un individuo di *H. formosa* Bergh, 1880, raccolto anch'esso nell'Australia occidentale, viene studiato e confrontato con individui raccolti nell'Oceano Indiano occidentale. Il confronto delle quattro nuove specie con le descrizioni originali e successive di *H. formosa* Bergh, 1880; *H. aurantiomaculata* Allan, 1932; *H. carlsoni* Rudman, 1978; *H. malesso* Carlson & Hoff, 2000; *H. stricklandi* Fahey & Gosliner, 1999; *H. bacalusia* Fahey & Gosliner, 1999; *H. diaphana* Fahey & Gosliner, 1999; *H. johnsonorum* Carlson & Hoff, 2000 and *H. batangas* Carlson & Hoff, 2000. La colorazione, il sistema riproduttivo e la morfologia radulare delle quattro nuove specie appare significativamente diversa da quelle precedentemente descritte nelle altre specie di *Halgerda*. Dati morfologici e anatomici di queste nuove specie vengono usati per ridefinire una filogenesi preliminare di questo genere. L'analisi filogenetica conferma la monofilia di *Halgerda* e i suoi rapporti con il genere *Asteronotus* Ehrenberg, 1831.

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INTRODUCTION

Previous workers have described species within the genus *Halgerda* from specimens collected throughout the tropical Indo-Pacific. These specimens have been collected from southern Africa, as the western-most locality, to Hawaii in the east. The type species, *Halgerda formosa* Bergh, 1880, was first described from a specimen collected from La Reunion. This species has since been collected from South Africa, Mauritius, Tanzania and Western Australia.

To date, five species of *Halgerda* have been photographed and collected from Western Australia. One of these species was originally thought (Wells & Bryce, 1993) to be *H. punctata* Farran, 1905, but was subsequently recognized as *H. formosa* by Fahey & Gosliner (1999a). The radula and reproductive anatomy of this specimen of Western Australian *H. formosa* is here examined and compared to the specimens collected from Mauritius (BMNH 2350) and southern Tanzania (CASIZ 099340). The Western Australian specimen (WAM S12385) has the same reproductive and radular morphology previously described for *Halgerda formosa* by Fahey & Gosliner (1999a), but some external color differences exist.

In addition, one of the species that was previously described as *H.* cf. *carlsoni* (Wells & Bryce, 1993) is identified as another new Western Australian species. *H. theobroma* has previously been recorded as *H.* sp., by Coleman, 1989. Three additional new species of *Halgerda*, all recently collected from Western Australia are also described. These new species have some external and/or internal similarities with other *Halgerda* species, and are compared. This brings to eight, the number of *Halgerda* species recorded from Western Australia.

SYSTEMATICS

Family Halgerdidae Odhner, 1926

Genus *Halgerda* Bergh, 1880

Type species: *Halgerda formosa* Bergh, 1880, by monotypy.

Halgerda formosa Bergh, 1880
(Figures 1, 2)

Halgerda sp. Coleman, 1989: 25, bottom photo, misidentification; not *Halgerda* Eliot, 1904.

Synonymy

Halgerda punctata Wells & Bryce, 1993: Plate 127, misidentification; not *H. punctata* Farran, 1905.

Material examined

WAM 1058-85, one specimen, dissected. Bundegi Reef, Exmouth Gulf, Western Australia. 1981. Photographed and collected by S. Slack-Smith and C. Bryce.

WAM S12385, two specimens, one dissected. Three rock reef, Dunsborough, Geograph Bay, Western Aus-

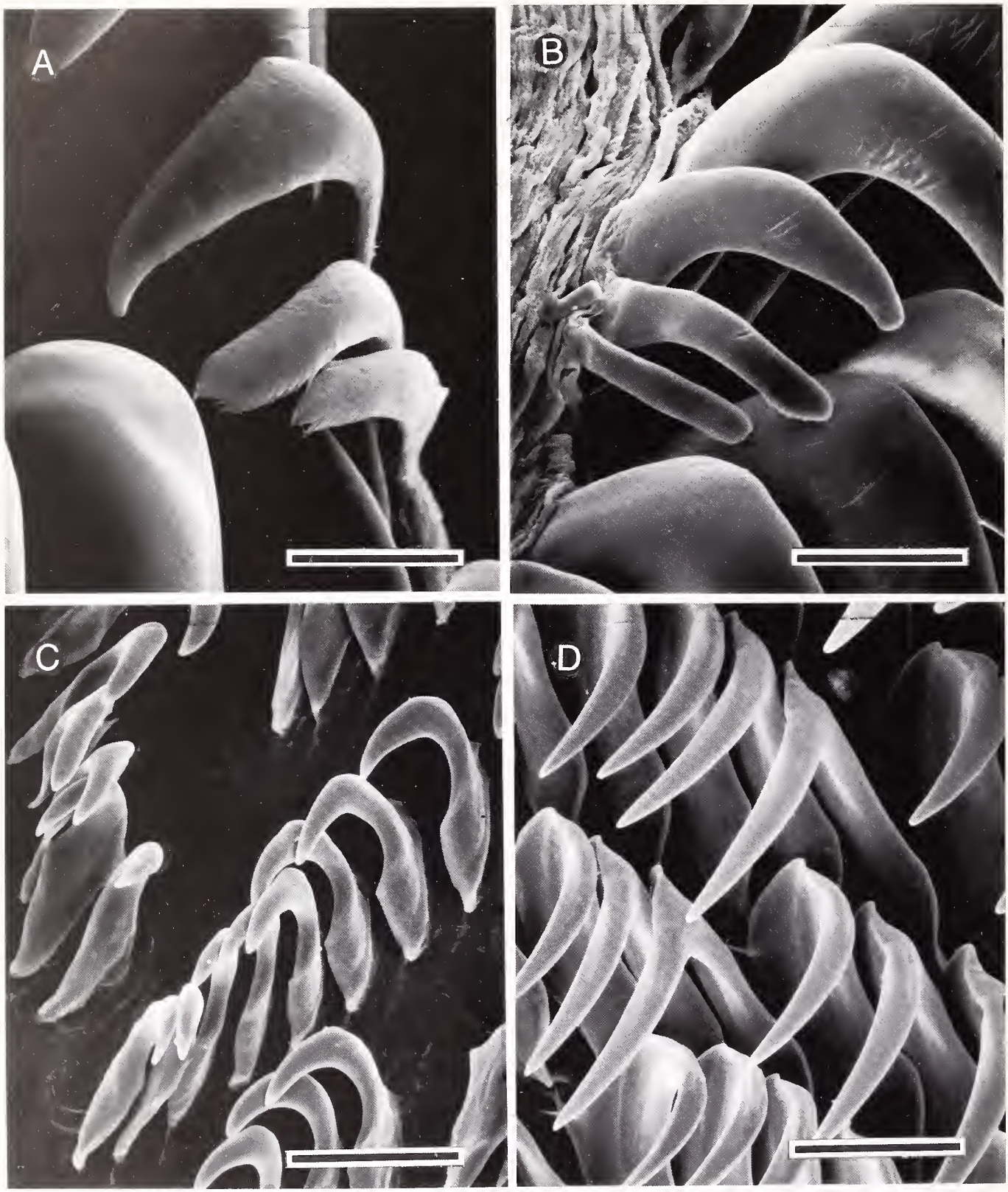

Figure 1. *Halgerda formosa* (WAM S12385). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 43 µm. B. Outer lateral teeth, scale = 20 µm. C. Inner lateral teeth, scale = 43 µm. D. Middle lateral teeth, scale = 75 µm.

tralia. January, 1978. Photographed and collected by C. Bryce and F. Wells.

External morphology

The preserved animals studied (WAMS 12385) each measured 15mm. The body is firm and smooth, but rigid. The body profile is high and the dorsum has a series of low, angled ridges arranged in a reticulate pattern. There are no conical tubercles at the junctions of the ridges. The ground color of the dorsum and foot is whitish with a gray tinge. The ridges are lined with yellow-orange, with shorter, thinner yellow-orange lines in the depressions between the ridges. There are no small white tubercles along the mantle margin as were found on specimens of *Halgerda formosa* from southern Tanzania and Mauritius (Fahey & Gosliner, 1999a). The mantle edge has a thin yellow-orange line around the circumference. Along the edge of the mantle are irregularly spaced, perpendicular black lines. There are some black spots on the dorsum between the ridges. The dark pigmentation on the viscera can be seen through the translucent notum.

The upright rhinophores are tapered towards the tips and there is black coloration on the club. The rhinophore base is white with a black line extending down the posterior side of the stalk. There are 19 transverse rhinophoral lamellae.

There are four bipinnate branchial leaves. The gills have black lined branches and the pigment encircles each branch tip. Within the gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is long and tubular with black coloration on both the posterior and anterior sides. The oral tentacles are short and digitform. Some dark spots on the ventral side of the foot are retained on the preserved animals. The tip of the foot, which extends beyond the mantle margin, has orange-yellow coloration on the edge.

Buccal armature

The buccal mass is not pigmented. The labial cuticle is smooth and devoid of rodlets. The radular sac is elongate, and the radular formula of the specimen is: 38x40.0.40 (WAM S12385). The three outer lateral teeth are degenerate (Figs 1A, B) and the first and second teeth from the outside of the row have short denticles. The inner lateral teeth (Fig. 1C) are arranged in a V-shaped angle on the radular ribbon. The inner laterals are hamate although the hook is much shorter than that of the middle lateral teeth (Fig. 1D). The middle lateral teeth are hamate with a wide, flattened base.

Reproductive system

The reproductive system is triaulic (Fig. 2). The ampulla is long and lies across the anterior of the female gland mass. The female gland mass is about the same size as the prostate gland. The ampulla has a slight narrowing as it enters the postampullary duct and bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. As the vas deferens separates from the ampulla, it widens into the large, glandular prostate that has two parts. The muscular portion of the ejaculatory duct leaves the prostate in a long, single duct with one half-loop, then widens into the expansive penial bulb. The short uterine duct emerges from the female gland mass and joins the receptaculum seminis duct near its junction with the duct from the bursa copulatrix. The receptaculum duct is long, convoluted and joins the oval receptaculum seminis with the larger, spherical bursa copulatrix adjacent to the vagina. The bursa is completely covered by the larger prostate. The vaginal duct, which emerges from the base of the bursa copulatrix, is short. There is a muscular sphincter at the entry to the vagina. The enlarged muscular region of the vagina constricts before its exit in the center of the genital atrium. Both the penis and the vagina are unarmed. The common genital atrium is wide and large.

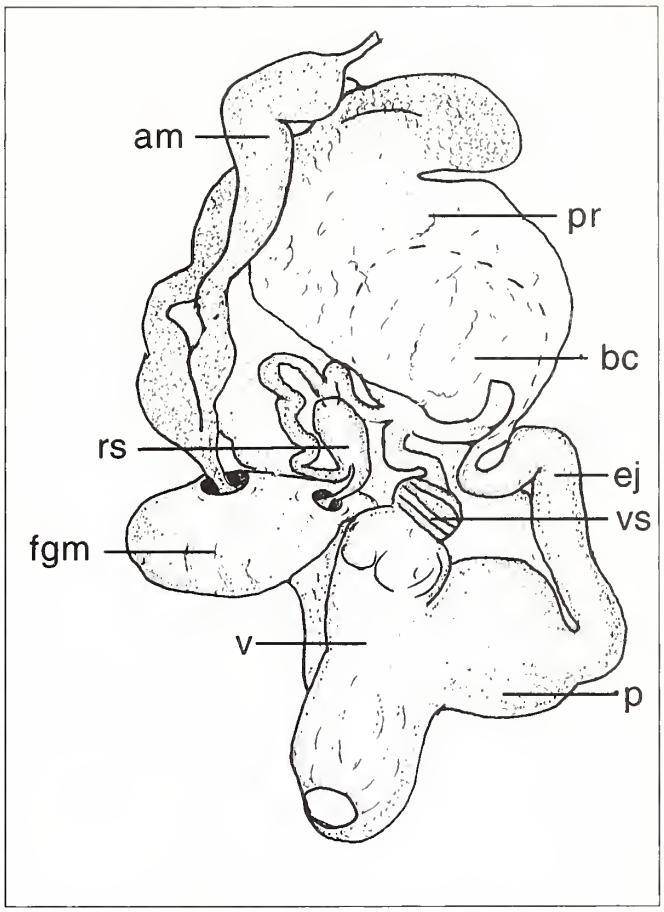

Figure 2. *Halgerda formosa* (WAM S12385). Reproductive system. am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vs = vaginal sphincter. scale = 1mm.

DISCUSSION

Bergh's original, (1880) detailed description of *Halgerda formosa* detailed the external morphology and descriptions and drawings of the radular and the reproductive anatomy. Examination and comparisons of specimens collected from South Africa, Mauritius, Tanzania and now, Western Australia confirm similar characteristics between them. Fahey & Gosliner (1999a) presented a detailed comparison of all specimens, but they excluded the radular and reproductive anatomy of the

Western Australian specimen, which had not been available for examination until recently.

The Western Australian specimen is confirmed to have the following reproductive similarities with the previously described specimens of *H. formosa*:

1) A long, tubular ampulla,

2) A large, muscular ejaculatory duct,

3) A thin-walled, bulbous vagina with a muscular sphincter at the opening of the short vaginal duct,

4) An expansive penial bulb that is separate from the vagina,

5) A glandular prostate that covers the bursa copulatrix.

There are slight differences in the external morphology of the animal found in Western Australia. While the Western Australian specimen has the characteristic irregularly spaced dark brown to black spots on the mantle, there are also dark brown, irregular streaks of color perpendicular to the mantle edge. The Western Australian specimen is also unique in having an orange mantle margin, orange coloration on the tip of the foot and a black line up the posterior side of each rhinophore.

The radular morphology of the Western Australian specimen is nearly identical to the drawings of Bergh's (1880) La Reunion specimen. The outer three teeth are degenerate, and the outer two have denticles. This is slightly different from Rudman's (1978) description of a Tanzanian specimen that shows the outer three degenerate teeth having no denticles. The denticles could easily be missed as they are slight, and almost non-existent on some outer lateral teeth.

From examination of the collected specimens, it appears that *Halgerda formosa* has a range of at least South Africa in the west, to Western Australia in the eastern Indian Ocean.

Halgerda gunnessi sp. nov.
(Figures 3A, 4, 5A)

Halgerda graphica Wells & Bryce, 1993, Plate 131; not *H. graphica* Basedow & Hedley, 1905.

Material examined

Holotype: WAM S12391, one specimen, 70 mm. Barney's Reef. Southwest tip of Rottnest Island, Western Australia. January, 1999. Photographed and collected by G. Gunness. Paratypes: WAM S12431, one specimen, 16 mm. Barney's Reef. Southwest tip of Rottnest Island, Western Australia. 19 December, 1999. Collected by S. Fahey. WAMS 12434, one specimen, 45 mm. Woodsy's, west end of Rottnest Island, Western Australia. 20 December 1999. Photographed and collected by G. Gunness. WAM S12435, one specimen, dissected, 40 mm. Woodsy's. West end of Rottnest Island, Western Australia. 20 December 1999. Collected by S. Fahey.

Distribution

This animal is known only from Western Australia (this study).

Etymology

This species is named for Graeme Gunness who first found this animal and was just as excited about it as the senior author. His interest and enthusiasm for diving are only surpassed by his hospitality.

Natural history

This animal is found at depths between 27 and 30 m, on limestone substrate that is covered with course sand, sponges, other invertebrates and a variety of algae. The areas generally have clear water with strong currents and high sea swells.

External morphology

The preserved holotype is 70 mm in length. The body profile is high (Fig. 3A) and the dorsum has a low, simply ridged pattern. There are no tubercles. There is a central ridge running the length of the dorsum and two perpendicular ridges evenly spaced along the mid dorsum. The central ridge and the mid-posterior ridge bifurcate as they near the mantle margin. The ridges have yellow crests that are outlined in white. The background color of the dorsum is gray-white with an overlay of chocolate brown. Between the ridges are secondary lines with the same color pattern as the ridges. Some of these lines connect to the ridges. The mantle margin has the same yellow coloration outlined in white. On the underside of the mantle and along the body sides are brown irregular spots. The foot margin is yellow. The gonadal pore has numerous brown striations radiating out from the opening. The oral tentacles are long and tapered, and the buccal mass has small brown dots.

The long rhinophores have a bulging club that is tapered at the tips. The club is angled posteriorly. There is dark brown to black coloration around the top half of the club up to the tip. The base is translucent white with brown splotches on the posterior side. There is a black line on the posterior side of the rhinophores that extends from the base to the tip.

The bipinnate gill lies flat over the dorsum and is moderately pinnate. Each of the four main gill rachae has a brown stripe on both the anterior and posterior sides. Within the gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is long and has brown pigment on the tip.

Buccal armature

The buccal mass is not pigmented. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the holotype is: 51x49.0.49 (CASIZ 117275) (Fig. 4). The three outer teeth are much smaller than the inner and middle lateral teeth and have no denticles (Fig. 4A). The 20 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Figs. 4B & C) and are arranged in a V-shaped pattern. The middle lateral teeth are hamate (Fig. 4D) with very long, pointed hooks. They have a flattened flange that overlaps the adjacent tooth.

Reproductive system

The reproductive system is triaulic (Fig. 5A). The long ampulla is tubular, curved in a half-loop and protrudes away from the bursa and prostate. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is about the same size as the prostate gland. As the short vas deferens separates from the ampulla, it widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well differentiated as in most other members of *Halgerda*. The muscular portion of the ejaculatory duct leaves the distal prostate in a long, single duct, that curves into three half-loops, then enters the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the spherical receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is very long and coiled. The spherical receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The prostate does not completely cover the bursa copulatrix as is common in other, more highly derived species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is long and thin. Near its exit, adjacent to the base of the male aperture, is a large sphincter prior to the bulbous vagina. The common genital aperture is wide and large. The opening of the female gland mass is adjacent to the genital aperture.

DISCUSSION

Halgerda gunnessi has unique external coloration among *Halgerda* species. However, due to some similarities in the ridge coloration, comparison is made with *H. johnsonorum* (Carlson & Hoff, 2000). In addition, due to some internal morphological similarities with *H. formosa* Bergh 1880, a comparison is made between these two species.

Carlson & Hoff (2000) described *H. johnsonorum* as having dark longitudinal lines often running mid-dorsally between ridges that are lined with yellow. *Halgerda gunnessi* also has a mid-dorsal ridge, but it is gray-white like the body, and has a yellow crest, outlined with white. *Halgerda gunnessi* has secondary lines with the same color pattern as the ridges, whereas the secondary lines of *H. johnsonorum* are dark, like the mid-dorsal ridges. Both species have brown spots along the sides of the body, under the mantle. *Halgerda gunnessi* has numerous, small dark lines perpendicular to the genital pore. *H. johnsonorum* has a few brown lines on the bottom of the foot. A few additional lines lead to the genital pore.

Both species have dark coloration on the rhinophores. *Halgerda gunnessi* has brown to black coloration on the top half of the club and brown splotches on the posterior side of the base, while *Halgerda johnsonorum* has brown spots covering the rhinophores. *Halgerda gunnessi* has a brown stripe on both the anterior and posterior sides of each gill rachis, whereas *H. johnsonorum* has brown spots on both sides of each rachis.

The reproductive anatomy differs significantly between these two species. The most significant difference is the large sphincter prior to the bulbous vagina of *Halgerda gunnessi*. *H. johnsonorum* does not have a sphincter at the end of the narrow vaginal duct, which widens only slightly at the genital atrium.

The radulae of these two species also differ significantly. *Halgerda gunnessi* has three small, simple outer teeth without denticles, whereas the six outer teeth of *H. johnsonorum* are smaller, and the three outer teeth are flattened with a bifid penultimate tooth.

Bergh's (1880) description of the radula of *Halgerda formosa* included 51 rows of hooked teeth, like *H. gunnessi*. However, Bergh reported 42 teeth per half-row and *H. gunnessi* has 49. *H. formosa* has three outer teeth denticulate (Bergh, 1880; Fahey & Gosliner, 1999a) or smooth (Rudman, 1978; present study). None of the outer lateral teeth of *H. gunnessi* are denticulate.

The reproductive system of *H. gunnessi* has some similarities to *H. formosa*. These are: both have a sphincter at the exit of the vaginal duct, prior to the vagina, both have a bulbous penis and a common genital atrium, and have elongate ejaculatory ducts and ducts connecting the receptaculum seminis and bursa copulatrix.

The reproductive morphologies of *H. gunnessi* and *H. formosa* differ in the following ways:

1) The prostate of *H. gunnessi* covers only half of the bursa copulatrix, whereas in *H. formosa*, the prostate completely covers the bursa.

2) The vagina in *H. gunnessi* is much shorter than in *H. formosa*. The vagina of *H. formosa* has two distinct chambers, separated by a constriction. *H. gunnessi* has a one-chambered bulbous vagina.

3) The vaginal duct of *H. gunnessi* is longer than that of *H. formosa*.

4) The ejaculatory duct of *H. formosa* is much thicker and longer than that of *H. gunnessi*.

5) The bursa copulatrix in *H. gunnessi* is much larger relative to the entire reproductive system, whereas in *H. formosa*, the bursa is not nearly as large.

The external morphologies of *H. gunnessi* and *H. formosa* differ in many ways. Among those differences are:

1) *H. gunnessi* lacks the small tubercles along the mantle edge as can be found on *H. formosa*.

2) *H. gunnessi* has overlying chocolate brown coloration on the dorsum, whereas *H. formosa* has irregularly spaced dark brown to black spots.

3) The ridges on the dorsum of *H. gunnessi* are very low whereas in *H. formosa* the ridges are higher and more distinct.

4) *H. gunnessi* has black coloration scattered around the base of the rhinophores, in addition to the dark coloration on the club. *H. formosa* also has the dark coloration on the club and a dark longitudinal line down the posterior side of the stalk.

5) The bulbous penis of *H. formosa* is proportionately much larger than that of *H. gunnessi*.

Halgerda theobroma sp. nov.
(Figures 3B, 5B, 6)

Halgerda sp., Wells & Bryce, 1993. Plate 130, Coleman, 1989. Page 26, middle photograph.

Material examined

Holotype: WAM S12314, one specimen, dissected. Mary's Reef, northeast side of Rottnest Island, Western Australia. 23 m depth. 26 December 1998. Collected by S. Fahey. Photo by C. Bryce of a second specimen, specimen lost. Paratypes: WAMS 12437, one specimen. Sam's, southwest side of Rottnest Island, Western Australia. 1 January 2000. Collected by S. Fahey. WAMS S12436, one specimen. 32 mm. Sam's, southwest side of Rottnest Island, Western Australia. 30 m depth. 1 January 2000. Collected by S. Fahey. WAM S12433, one specimen, 18 mm. Woodsy's, west end of Rottnest Island, Western Australia. 30 m depth. 20 December 1999. Collected by S. Fahey.

Distribution

This animal is known only from Western Australia.

Etymology

The trivial name *Theobroma* is a Latin word for the genus of cocoa. The name was chosen for the chocolate brown color that predominates on the dorsum.

Natural history

This animal was found on a limestone substrate that was covered with course sand and a variety of algae and sponges. The original specimen was found at 6 meters depth on similar substrate, in an area with caves and underhangs encrusted with sponges, bryozoans and other sessile animals (C. Bryce, pers. com). The area of Rottnest Island where this animal has been found has generally clear water with minimal water movement except during the winter storms when there is considerable sea chop.

External morphology

The preserved animal studied is 20 mm in length. Although the body profile is slightly arched (Fig. 3B), the

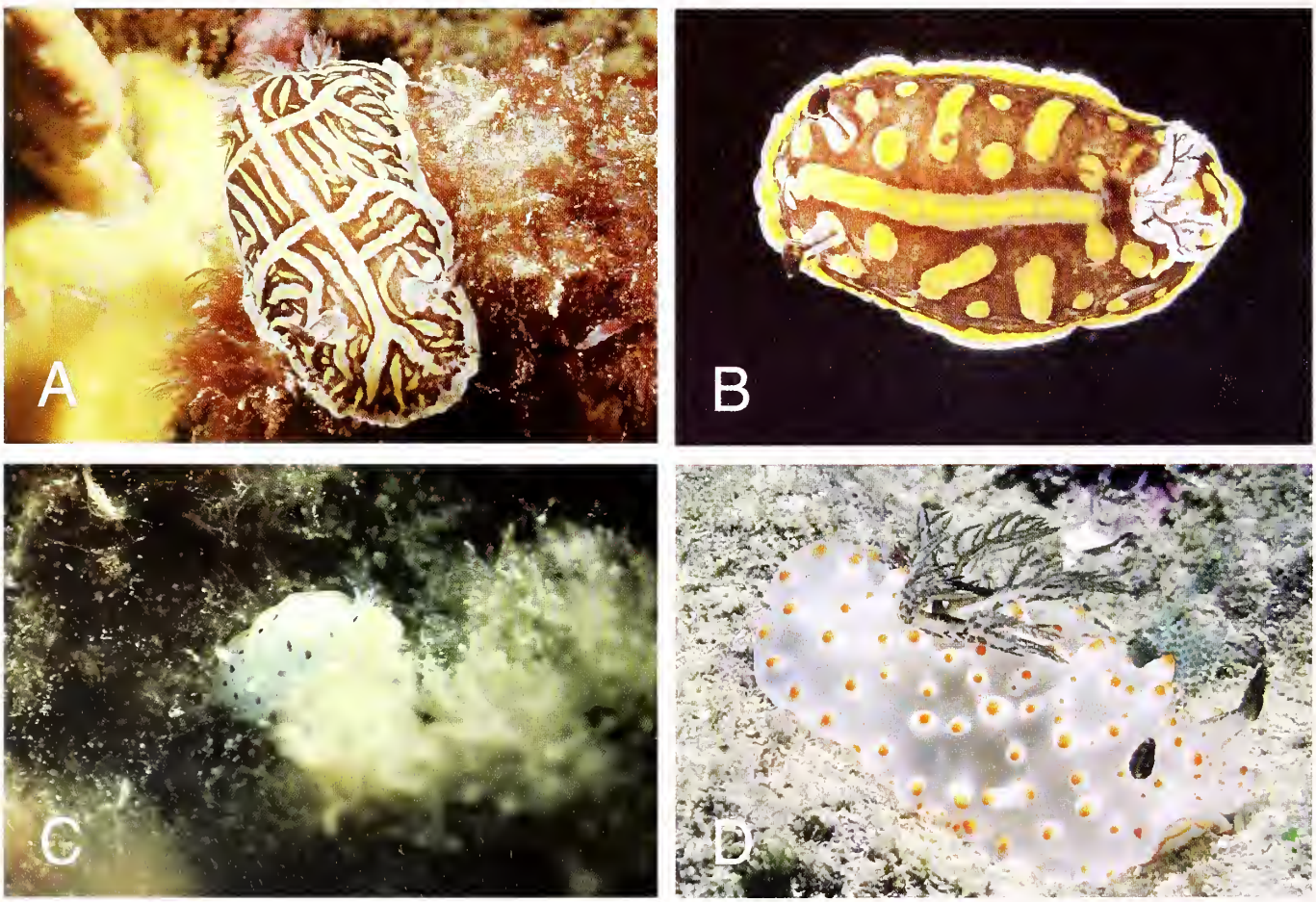

Figure 3. Living Animals. A. *Halgerda gunnessi* sp. nov. (WAMS 12391). Specimen, 70 mm, from Rottnest Island, Western Australia. 27 m depth, January, 1999. Photo by G. Gunness. B. *Halgerda theobroma* sp. nov. same as (WAMS 12314). Specimen, 20 mm, from Rottnest Island, Western Australia. 21 m depth, December, 1998. Photo by C. Bryce of lost specimen. C. *Halgerda maricola* sp. nov. (WAMS 12318). Specimen, 17 mm, from Rottnest Island, Western Australia. 23 m depth, December, 1998. Photo by G. Gunness. D. *Halgerda bryci* sp. nov. (WAMS 12392). Specimen, 50 mm, from Brigadier Island, Dampier Archipelago, Western Australia.10 m depth, April, 1987. Photo by C. Bryce.

animal does not have the high body form common in many other *Halgerda* species. The body is more flaccid than other *Halgerda* species, and the mantle touches the substrate as it crawls. The dorsum also does not have the characteristic ridge pattern of other *Halgerda* species, but it does have one wide central, yellow ridge on the mid dorsum. This yellow central ridge is outlined in white. The ground color of the dorsum is transparent white, but is almost entirely covered with chocolate brown. There are round, slightly raised, yellow splotches of color evenly spaced along the outer edge of the mantle and short, wide streaks of yellow which lie almost perpendicular to the central ridge. The yellow splotches are also found on either side of the central ridge and around the gill pocket which has a yellow rim. There is a wide, yellow band along the submarginal mantle edge, with a narrow white band on the extreme edge. The foot is translucent white with a gray cast and it has a yellow margin. The oral tentacles are long and tapered.

The long rhinophores have a bulging club and are tapered at the tips. The club is angled posteriorly. There is dark brown to black coloration around the top half of the club up to the tip. The base is translucent white. There is a black line on the posterior side of the rhinophores that extends from the base to the tip.

The bipinnate gill is moderately pinnate and the branchia are translucent white with black lines that extend from the base to the tips on the exterior sides. Each of the three main leaves divides into two branches, with the posterior two more highly pinnate than the anterior one. Within each gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is long and translucent white.

Buccal armature

The buccal mass is not pigmented. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the holotype is: 38x40.0.40 (WAM S12314) (Fig. 6). The three outer teeth are much smaller than the inner and middle lateral teeth and have no denticles (Fig. 6A). The 17 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Fig. 6B) and are arranged in a V-shape. The middle lateral teeth are hamate (Fig. 6C) with a long, pointed hook and a wide, flattened base.

Reproductive system

The reproductive system is triaulic (Fig. 5B). The ampulla is tubular, elongate and protrudes away from the bursa and prostate. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is larger than the prostate gland. As the short vas deferens separates from the ampulla, it widens into the glandular prostate. The prostate consists of two distinct glandular types and they are well differentiated as in most other members of *Halgerda*. The muscular portion of the ejaculatory duct leaves the distal prostate in a long, single duct, that curves into one half-loop, then enters the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the spherical receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is very long and coiled. The spherical receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The prostate completely covers the bursa copulatrix as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is short and wide. Near its exit adjacent to the base of the male aperture, is a large obviously glandular portion of the bulbous vagina. The common genital atrium is wide and large. The opening of the female gland mass is adjacent to the genital aperture.

DISCUSSION

Although the external coloration is unique among *Halgerda*, *H. theobroma* has some reproductive similarities to other *Halgerda* species. The most noticeable similarity with other *Halgerda* species is the distinctive glandular vagina. This feature is shared by *H. aurantiomaculata* Allan, 1932; *H. carlsoni* Rudman, 1978; *H. malesso* Carlson & Hoff, 1993; *H. stricklandi* Fahey & Gosliner, 1999; *H. bacalusia* Fahey & Gosliner, 1999; *H. diaphana* Fahey & Gosliner, 1999 and *H. batangas* (Carlson & Hoff, 2000). *Halgerda theobroma* is compared with these species due to this particular similarity.

When comparing external coloration, the following differences are noted: Unlike the other seven species of *Halgerda* with a glandular vagina, *Halgerda theobroma* has no rounded dorsal tubercles with orange pigmentation. And although all these species share a gray-white background color, *Halgerda theobroma* has a unique overlay of chocolate brown pigmentation. In addition, most of the other species, except *Halgerda stricklandi* and *H. bacalusia* have dark speckles on the rhinophores and gills.

There are also radular differences among these species. Only *Halgerda theobroma* has simple hamate outer lateral teeth. The other species all have fimbriate outer teeth. In addition, the tooth rows are arranged in a V-shaped pattern in *Halgerda theobroma*. Only *H. diaphana* shares this pattern. The tooth rows of all other species are straight.

The reproductive differences among the eight species are as follows:

1) The vaginal ducts of *H. malesso* and *H. batangas* are extremely wide as compared to *H. theobroma*, *H. aurantiomaculata*, *H. stricklandi* and *H. carlsoni*. The vaginal ducts of *H. stricklandi* and *H. carlsoni* are similar and both are longer and narrower than that of *H. theobroma*, *H. malesso* and *H. batangas*.

2) The penis and the vagina are not joined basally into a common genital atrium in *H. malesso* and *H. aurantiomaculata*, whereas in *H. theobroma*, *H. stricklandi*, *H. batangas*, and *H. carlsoni* they share a common opening.

3) The penis in *H. aurantiomaculata*, *H. malesso* and *H. batangas* is more bulbous than that of *H. theobroma*, *H. stricklandi*, and *H. carlsoni*, all which have a more tubular penis, that is wider than the vagina. Only *H. bacalusia* has a penis

Figure 4. *Halgerda gunnessi* sp. nov. (WAM S12391). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 60 μm. B. Inner lateral teeth, scale = 150 μm. C. Inner lateral teeth, scale = 60 μm. D. Middle lateral teeth, scale = 150 μm.

that is the same size as the vagina. In addition, the penis of *H. theobroma* is larger than that of *H. stricklandi*, *H. bacalusia*, *H. carlsoni* and *H. batangas*.

4) *H. malesso*, *H. batangas*, *H. stricklandi*, and *H. bacalusia* all have dark pigmentation on the genital atrium, however, the location of the pigmentation differs. In *H. malesso*, the pigmentation is at the top of the atrium, equidistant from both the vagina and penial openings. In *H. bacalusia* the coloration lines some of the genital vestibular folds. In *H. stricklandi*, the pigmentation lies in the penis, at the junction with the vagina. *H. theobroma*, *H. aurantiomaculata* and *H. carlsoni* have no pigmentation.

5) The bursa copulatrix of *H. theobroma* is larger, relative to the overall reproductive system than that of any of the other four species.

Halgerda maricola sp. nov.
(Figures 3C, 5C, 7)

Material examined

Holotype: WAMS 12318. One specimen, dissected. Mary's Reef, northeast side of Rottnest Island, Western Australia. 23 m depth, 26 December 1998. Photographed by G. Gunness. Collected by S. Fahey. Paratype: WAM 133-87, one specimen, dissected. Between Cervantes Island and Cervantes, Western Australia. 29 April 1987. Collected by C. Bryce.

Distribution

This animal is known only from Western Australia (this study).

Etymology

The trivial name *maricola* is derived from the locality where the specimen was found (Mary's Reef), which was named after Mary Gudgeon, a good friend, an avid diver and underwater photographer. The Latin extension –cola means "inhabitant of".

Natural history

The holotype was found on a vertical limestone substrate that was covered with algae and sponges.

External morphology

The preserved animal studied is 17 mm in length. It has a low body profile with the characteristic reticulated ridge pattern of other *Halgerda* species, although the ridges are extremely low. The background color of the dorsum is white and the ridges have very thin orange crests. There are small black dots in the concavities of the ridges. The mantle margin is lined in yellow, as is the foot margin.

The rhinophores are long with a bulging club that has a tapered tip. The club is angled posteriorly. The ground color is translucent white and the top of the club has dark pigmentation.

The bipinnate gill is divided into four branches that are moderately pinnate. The background color is translucent white and there are dark splotches of color on the posterior sides and at the tips of each gill rachis. Within each gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is translucent white.

Buccal armature

The buccal mass is not pigmented. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the holotype is: 40x34.0.34 (WAM S12318) (Fig. 7). The three outer teeth are much smaller than the inner and middle lateral teeth and have no denticles (Fig. 7A). The 14 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Fig. 7B). The second tooth in some rows is bifid. The middle lateral teeth are hamate (Fig. 7C) and have long, pointed hooks. They have flattened bases which widen slightly.

Reproductive system

The reproductive system is triaulic (Fig. 5C). The short ampulla is tubular, wide and protrudes away from the bursa and prostate. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is larger than the prostate gland. As the short vas deferens separates from the ampulla, it widens into the glandular prostate. The prostate consists of two distinct glandular types that are well differentiated as in most other members of *Halgerda*. The muscular portion of the ejaculatory duct leaves the distal prostate in a long, single duct, that curves into one half-loop, then enters the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the pyriform receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is very long and curved. The pyriform receptaculum seminis is much smaller than the thin-walled spherical bursa copulatrix. The prostate completely covers the bursa copulatrix as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is short and wide. Near its exit adjacent to the base of the male aperture, is a large obviously glandular portion of the bulbous vagina. The genital aperture is wide and large. The opening of the female gland mass is adjacent to the genital aperture.

Discussion

Because of the similarities in the external morphologies of *Halgerda maricola* and *H. formosa*, the two species are compared here. First, the similarities are presented:

1) Both specimens have a series of low, angled ridges, with no tubercles at the junctions of the ridges. The ridges are lined with yellow or yellow-orange. The body color of the two species is white with a grayish tinge.

2) Along the edge of the mantle and on the foot are irregularly spaced, dark brown to black spots. Both species also have yellow or yellow-orange mantle and foot margins.

3) The rhinophores of both species are tapered and have black coloration subapically.

4) The gills of both have black coloration on the leaves.

The external differences that can be detected between the two species are as follows:

1) *Halgerda formosa* has dark pigmentation on the tips and the stalks of the rhinophores, whereas the dark pigmentation on the rhinophores of *H. maricola* is confined to the tips.

2) The dark spots on the dorsum of *H. maricola* are consistently located within the ridge depressions while the spots on *H. formosa* are randomly scattered, usually closest to the mantle edge and can overlap the yellow ridge crests.

3) *Halgerda formosa* usually has small, marginal tubercles but *H. maricola* does not.

4) The tips of the gills of *H. maricola* are black whereas *H. formosa* has white gill tips.

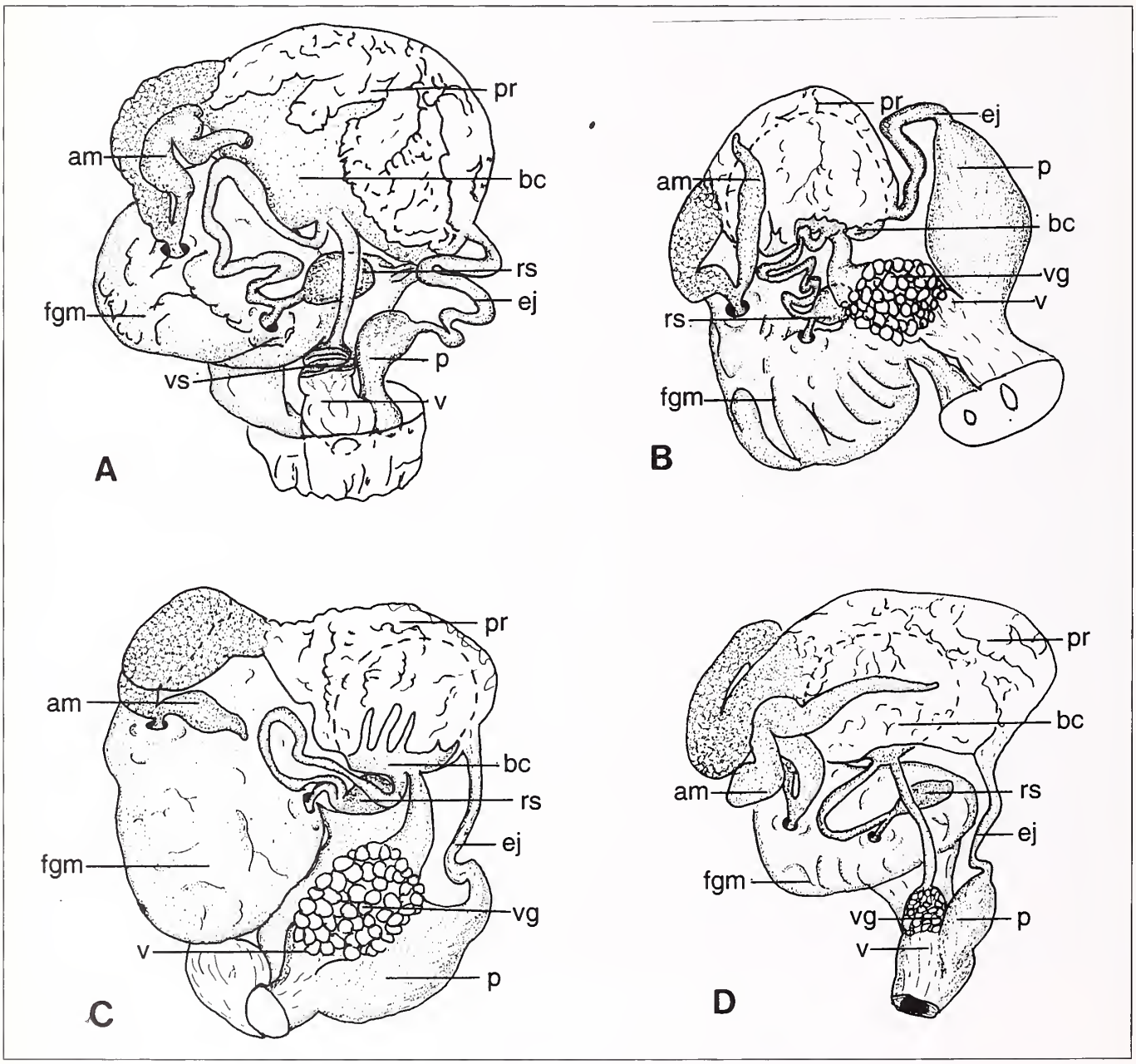

Figure 5. Reproductive systems. A. *Halgerda gunnesii* sp. nov. (WAM S12391). B. *Halgerda theobroma* sp. nov. (WAM S12314) C. *Halgerda maricola* sp. nov. (WAM S12318) D. *Halgerda bryci* (WAM S12392). am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vg = vaginal gland, vs = vaginal sphincter. scale = 1mm.

The reproductive morphologies of *H. maricola* and *H. formosa* differ significantly.

1) *H. maricola* has a large vagina that is glandular whereas *H. formosa* has a vaginal sphincter and the vagina is not glandular.

2) *H. maricola* has a short, wide vaginal duct, whereas *H. formosa* has a short, narrow duct.

3) *H. maricola* has a long ejaculatory duct, whereas *H. formosa* has an ejaculatory duct that is twice the length, and curves back on itself.

4) *H. maricola* has a short ampulla, whereas *H. formosa* has a long ampulla.

Halgerda brycei sp. nov.
(Figures 3D, 5D, 8)

Halgerda cf. *carlsoni* Wells & Bryce, 1993, Plate 129; not *H. carlsoni* Rudman, 1978.

Material examined

Holotype: WAM S12392. Brigadier Island, Dampier Archipelago, Western Australia. 2 April 1987. Photographed and collected by C. Bryce & F. Wells. Paratypes: WAM S12393. One specimen, dissected. Brigadier Island, Dampier Archipelago, Western Australia. 2 April 1987. Photographed and collected by C. Bryce & F. Wells.

WAM 459-93. One specimen. Monte Bello Islands, Western Australia. 24 August 1993. 7-13 m depth. Collected by C. Bryce & F. Wells. WAM S12384. One specimen. North Murion Island, Northwest Cape, Western Australia. 26 August 1995. 8 m depth. Collected by C. Bryce & M. Hewitt.

Distribution

This animal is known only from Western Australia.

Etymology

The trivial name *brycei* is given in honor of Clay Bryce of the Western Australian Museum who first found this species. Clay has also been a source of great assistance to the authors and actively engaged in nudibranch research. His generosity and hospitality in Western Australia are most appreciated.

Natural history

The holotype was found on a subtidal reef with a covering of calcarious sand and algal turf. Nearby were isolated coral heads and small encrusting sponges scattered about and other sessile animals in reef holes and under the coral heads. The area where it was found is prone to turbid water incursions on an out-going tide which can be strong (C. Bryce, pers. com).

External morphology

The preserved animals studied are 50 and 35 mm in length. The body profile is high, but it does not have obvious ridges as is typical of other *Halgerda* species. The dorsum is covered with angled tubercles that are high and tapered near the center of the dorsum, and lower nearer the mantle margin. The background color of the dorsum is translucent white. There is no other coloration on the dorsum between the pronounced tubercles. The tubercles each have an orange tip, below which is a bright white ring. The foot margin is orange and the oral tentacles are long and tapered.

The rhinophores are long, tapered and angled posteriorly. There is dark brown coloration surrounding the top half of the club up to and including the tip. The base is translucent white, with no dark spots. There is a black line on the posterior side of the rhinophores that extends from the base to the tip.

The white, translucent bipinnate gill is large, moderately pinnate and has four branchial leaves. There are brown spots scattered over the length of each branch, from the base to the tips. Within each gill rachis are numerous flattened, translucent structures that are glandular. The anal papilla is long and has black coloration on the tip.

Buccal armature

The buccal mass is not pigmented. The labial cuticle is smooth and devoid of any jaw rodlets. The radular sac is elongate and extends well behind the posterior end of the buccal mass. The radular formula of the paratype (50 mm) is: 65x54.0.54 (WAM S12392) (Fig. 8). The three outer teeth are much smaller and thinner than the inner and middle lateral teeth and have denticles (Fig. 8A). The 5 or so inner lateral teeth are smaller and have shorter hooks than the middle lateral teeth (Fig. 8B). The inner teeth are flat except for the hook. The middle lateral teeth are hamate (Fig. 8C) and are flat from the midpoint to the base. This allows them to overlap each other considerably, giving the appearance of piano hammers.

Reproductive system

The reproductive system is triaulic (Fig. 5D). The ampulla is long, tubular, curved in a half-loop and protrudes away from the bursa and prostate. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The female gland mass is proportionally smaller than the prostate gland. As the short vas deferens separates from the ampulla, it widens into the glandular prostate. The prostate consists of two distinct glandular types that are well differentiated as in most other members of *Halgerda*. The muscular portion of the ejaculatory duct leaves the distal prostate in a long, narrow, single duct that curves into the wide penial bulb. The short uterine duct emerges from the female gland mass and joins the pyriform receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is long and curved. The pyriform receptaculum seminis is much smaller than the thin-walled, spherical bursa copulatrix. The prostate completely covers the bursa copulatrix as is common in other species of *Halgerda*. The vaginal duct that emerges from the base of the bursa copulatrix is long and thin. Near its exit

Figure 6. *Halgerda theobroma* sp. nov. (WAM S12314). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 30 μm. B. Inner lateral teeth, scale = 75 μm. C. Middle lateral teeth, scale = 75 μm.

Figure 7. *Halgerda maricola* sp. nov. (WAM S12318). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 43 µm. B. Inner lateral teeth, scale = 43 µm. C. Middle lateral teeth, scale = 75 µm.

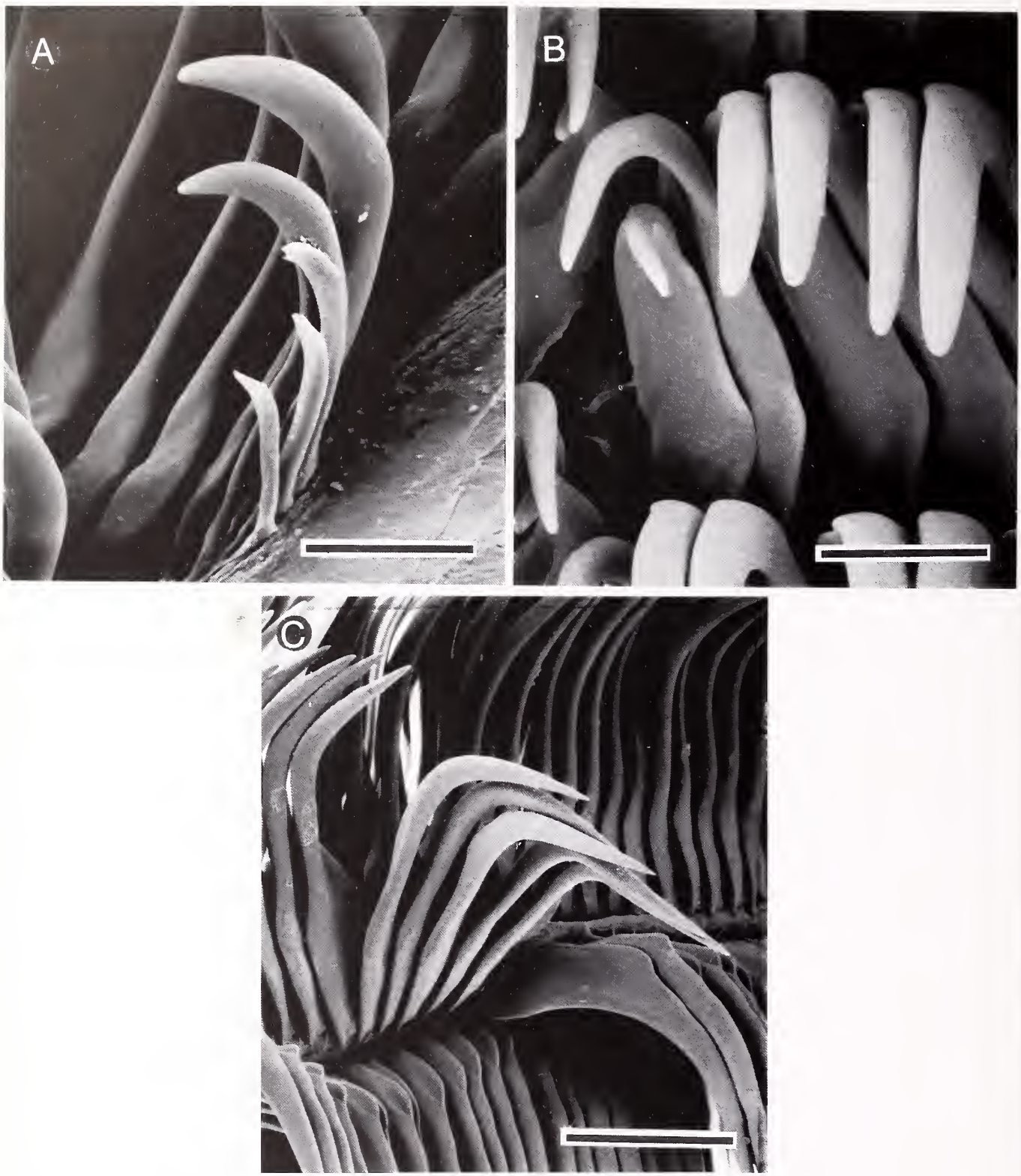

Figure 8. *Halgerda brycei* sp. nov. (WAM S12392). Scanning electron micrographs of radula. A. Outer lateral teeth, scale = 43 µm. B. Inner lateral teeth, scale = 30 µm. C. Middle lateral teeth, scale = 150 µm.

adjacent to the base of the male aperture, is a large, obviously glandular portion of the bulbous vagina. The genital aperture is wide and large. The opening of the female gland mass is adjacent to the genital aperture.

DISCUSSION

Halgerda brycei has some similar external characteristics with four other *Halgerda* species: *H. batangas* (Carlson & Hoff, 2000); *H. stricklandi* Fahey & Gosliner, 1999; *H. malesso* Carlson & Hoff, 1993 and *H. carlsoni* Rudman, 1978. These four species are compared to *H. brycei* because of their external similarities. These similarities include rounded, orange tipped tubercles, black pigmentation on the rhinophore club, dark lines on the gill leaves (except *H. malesso* and *H. carlsoni*), and a colored foot margin.

Halgerda stricklandi, H. malesso and *H. carlsoni* all have the same smooth but firm, high body profile with rounded tubercles tipped with orange scattered over the dorsum. All have orange or red (*H. carlsoni*) spots or lines scattered between the tubercles. *Halgerda brycei, H. batangas* and *H. carlsoni* have white coloration below the orange tubercle tips. *Halgerda malesso* and *H. batangas* both have a network of orange lines between the ridges. *Halgerda brycei* does not have orange spots between the tubercles, nor any secondary orange lines. All five of these species have an orange or red (*H. carlsoni*) foot margin and all have a white to gray-white background color.

Halgerda brycei differs from *H. batangas, H. stricklandi, H. malesso* and *H. carlsoni* in several distinct ways:

1) The rhinophores of all five species are long and tapering, with the club angled posteriorly. The rhinophores of *H. brycei* have a white base and black coloration circling the club. There is a black line on the posterior side. The rhinophores of *H. stricklandi* have a yellowish club and black-edged lamellae. There is also a black line extending the length on the posterior side of this species. *Halgerda batangas*, *H. malesso* and *H. carlsoni* have brown spots with brown lamellae and lack a line on the posterior side.

2) The four gill branchia of *H. brycei* have brown coloration scattered the length of each. The dark spots on *H. batangas*, *H. malesso* and *H. carlsoni* are smaller and more uniform than those of *H. brycei*. The four gill branchia of *H. stricklandi* are outlined with black on the posterior side and there are black spots on the anterior side only.

3) All five species have a glandular portion of the vagina, but the vaginal duct of *H. malesso* is extremely wide as compared to *H. brycei*, *H. stricklandi*, *H. carlsoni* and *H. batangas*. The vaginal ducts of *H. brycei, H. stricklandi* and *H. carlsoni* are similar and are narrower than that of *H. malesso* or *H. batangas*.

4) The penis and vagina are joined basally into a common atrium in *H. brycei, H. batangas*, *H. stricklandi* and *H. carlsoni*. *H. malesso* does not have a common genital atrium. The penis in *H. malesso* and *H. batangas* is more bulbous than that of *H. brycei, H. stricklandi* and *H. carlsoni*, all which have a more tubular penis, that is only slightly larger than the vagina.

5) *Halgerda carlsoni*, *H. malesso* and *H. stricklandi* have dark pigmentation on the genital atrium, however the location of the pigmentation differs. *H. batangas* has short brown streaks lining the genital atrium. *Halgerda brycei* lacks dark pigmentation on the genital atrium.

6) The three outer teeth of *H. brycei, H. stricklandi, H. malesso* and *H. carlsoni* are smaller than the middle and inner lateral teeth. The four outer teeth of *H. bantagas* are reduced in size. *Halgerda batangas* has a denticulate third outer lateral tooth. All three outer teeth of *H. stricklandi* are denticulate whereas in *H. malesso*, only two are denticulate and the third is simple. The outer most teeth of *H. batangas* are rodlike, with the second and third teeth are bifid. Rudman (1978) reported the three outer teeth of *H. carlsoni* from Fiji as degenerate and not denticulate. However, specimens examined from Papua New Guinea had three denticulate outer teeth. In addition, *H. stricklandi* and *H. batangas* have very long hamate middle lateral teeth with broad, flat bases and much thinner hooks than those of *H. malesso* and *H. carlsoni*. Both *H. carlsoni* and *H. malesso* have very similarly shaped inner and middle lateral teeth.

PHYLOGENETIC ANALYSIS

Previous literature and direct observation and dissection of 19 species of *Halgerda* and members of the outgroup have provided the information on the characters for the study of the phylogenetic relationships of *Halgerda* species. To establish the polarity of the morphological characters used in this study, one outgroup, *Asteronotus* was selected based on a review of the anatomical characters. The following characters were considered for use in the present analysis, based on this review. Characters in parentheses were included in the parsimony analysis, and determined to be phylogenetically uninformative.

1. Rhinophores.—All species of *Halgerda* have elongate rhinophores. The outgroup taxon, *Asteronotus* has short rhinophores and this character state is considered plesiomorphic.

2. Ridges.—All *Halgerda* have dorsal ridges. These ridges can be low-lying and almost level with the rest of the notum or they can be quite high and distinct. *Asteronotus* does not have ridges. The presence of low or non-existent ridges is considered the plesiomorphic state.

3. Tubercles.—Rounded dorsal tubercles are absent in 11 *Halgerda* species. Distinct rounded tubercles are present in ten *Halgerda* species, while pointed tubercles are present on another six species. *Asteronotus* has low, rounded tubercles, connected in concentric circles. The presence of low or absent tubercles is considered plesiomorphic.

4. Small marginal tubercles.—Small tubercles are found along the mantle edge of four species of *Halgerda*: *H. brunneomaculata* Carlson & Hoff, 1993, *H. formosa*, *H. tessellata* Bergh, 1880 and *H. toliara*. The outgroup taxon, *Asteronotus* does not have these marginal tubercles, and their presence is considered apomorphic.

5. Caryophyllidia.—No species of *Halgerda* have caryophyllidia. This character was considered, but then not included in

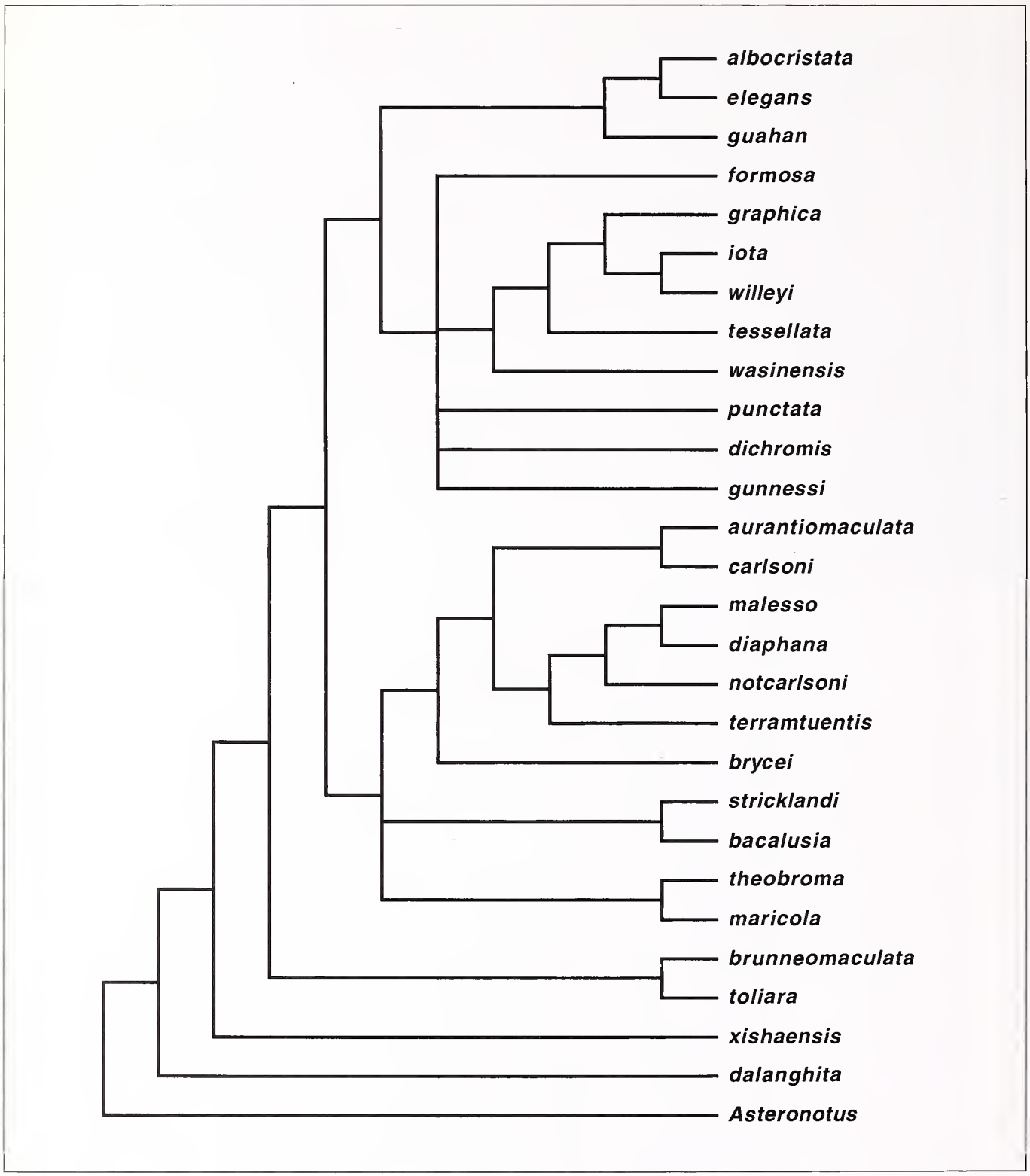

Figure 9. Phylogeny of *Halgerda*. Strict consensus of 6 most parsimonious trees. *Asteronotus* was chosen as the outgroup to polarize the characters.

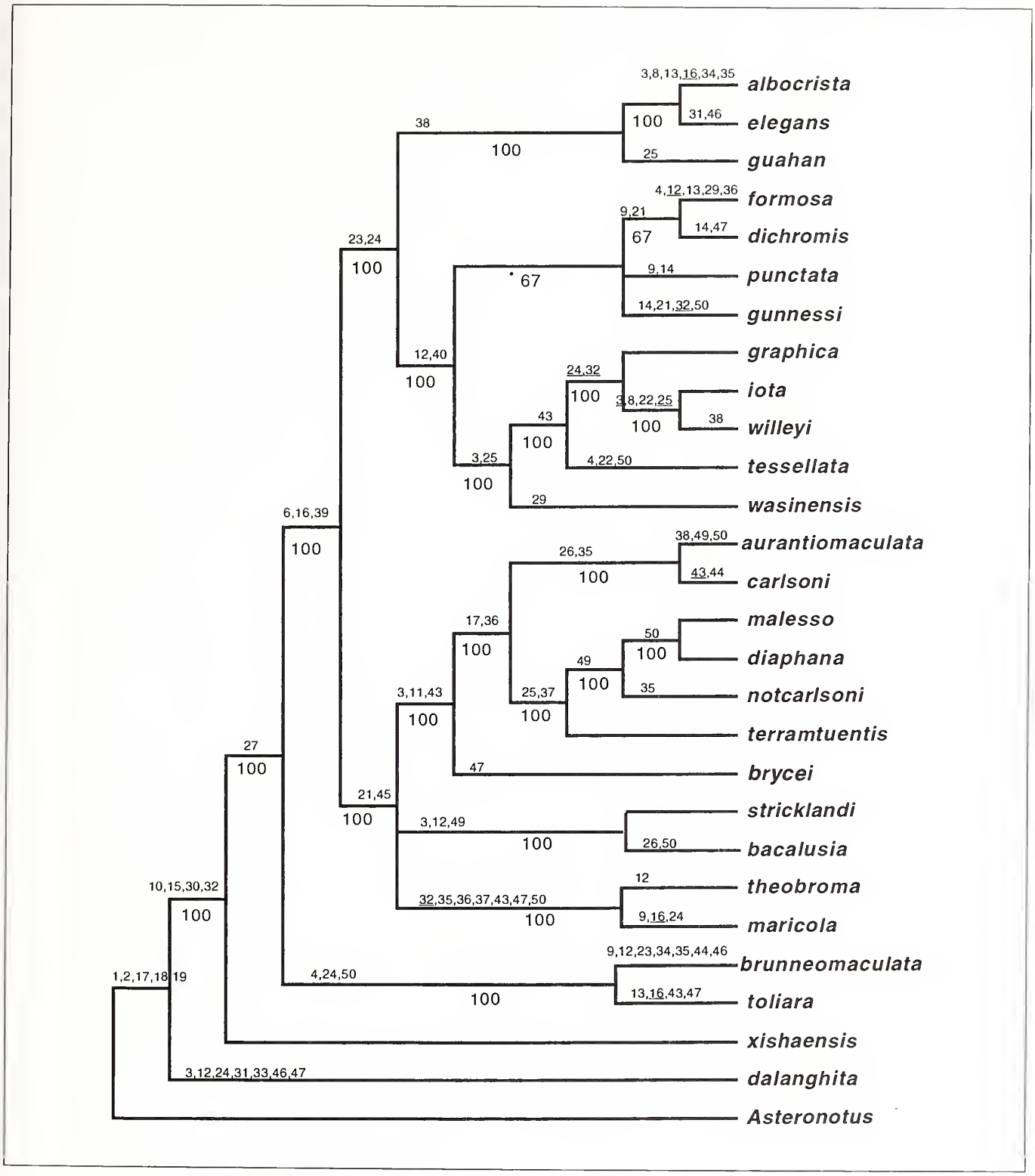

Figure 10. Phylogeny of *Halgerda*. Majority rule of 6 most parsimonious trees. Numbers above the branches refer to characters in Table 1. Underlined numbers indicate reversals. Numbers below the branches indicate the percent support for that branch.

Table 1. Characters and states considered for the phylogeny of *Halgerda*

	Character	Plesiomorphic	Apomorphic
1.	Rhinophores.—	0=short	1=elongate
2.	Ridges.—	0=absent	1=present
3.	Tubercles.—	0=absent/low	1=rounded, 2=pointed
4.	Small marginal tubercles.—	0=absent	1=present
5.	Caryophyllidia.—	0=present	1=absent
6.	Body color.—	0=reddish or orange	1=whitish
7.	Ridge color.—	0=body color	1=orange/yellow, 2=white
8.	Black marginal lines.—	0=absent	1=present
9.	Black spots.—	0=absent	1=present
10.	Gill branching.—	0=tripinnate	1=bipinnate
11.	Gill spots.—	0=absent	1=present
12.	Gill stripes.—	0=absent	1=present
13.	Gill tip color.—	0=white	1=black
14.	Gill shape.—	0=erect	1=flat
15.	Gill pinnation.—	0=highly pinnate	1=moderately, 2=sparsely pinnate
16.	Rhinophore base color.—	0=Same as body color	1=black blotches, 2=black spots 3=black stripes
17.	Rhinophore pigment.—	0=random	1=speckles
18.	Rhinophore bulb color.—	0=White	1=black
19.	Gill glands.—	0=Same as gill color	1=opaque
20.	Oral tentacles shape.—	0=short and rounded	1=long and tapered
21.	Foot border color.—	0=absent	1=present
22.	Foot lines.—	0=absent	1=present, 2=band
23.	Foot spots.—	0=absent	1=present
24.	Body shape.—	0=broad	1=elongate
25.	Secondary orange lines.—	0=absent	1=present
26.	Orange dots on dorsum.—	0=absent	1=present
27.	Radula sac shape.—	0=short	1=elongate
28.	Teeth rows.—	0=straight across	1=v-shaped
29.	Buccal mass.—	0=unpigmented	1=pigmented
30.	Radula shape.—	0=square	1=rectangular
31.	Middle lateral teeth.—	0=hamate	1=elongate, 2=both
32.	Outer lateral teeth shape.—	0=hamate	1=fimbriate
33.	Outer lateral teeth size.—	0=smaller than middle laterals	1= same size as middle laterals
34.	Fimbriate tooth length.—	0=short	1=elongate
35.	Ampulla length.—	0=long	1=short
36.	Vaginal duct length.—	0=elongate	1=short
37.	Vaginal duct shape.—	0=narrow	1=wide
38.	Vagina duct termination.—	0=enters common atrium	1=separate duct
39.	Vaginal base shape.—	0=narrow	1=wide
40.	Vaginal sphincter.—	0=absent	1=present
41.	Prostate.—	0=one part	1=two parts
42.	Differentiation of prostate.—	0=poorly differentiated	1=well differentiated
43.	Ejaculatory duct.—	0=elongate	1=short
44.	Receptaculum seminis.—	0=smaller than bursa	1=same size as bursa
45.	Tubercular vaginal glands.—	0=absent	1=present
46.	Penis shape.—	0=bulbous	1=tubular
47.	Uterine duct insertion.—	0=more distal	1=base of rs
48.	Prostate size.—	0=smaller than female gland mass	1=equal to female gland mass
49.	Atrium pigment.—	0=absent	1=present
50.	Mantle margin.—	0=absent	1=orange or yellow, 2=white line

the analysis since neither the outgroup chosen, *Asteronotus* nor the taxa being studied have caryophyllidia.

6. Body color.—The plesiomorphic state of an orange-yellow or reddish body color is shared by the outgroup taxon and four *Halgerda* species: *H. brunneomaculata, H. xishaensis* Lin, 1975, *H. dalanghita* and *H. toliara*. All other *Halgerda* have a white to gray-white background color.

7. Ridge color.—Three *Halgerda* have white dorsal ridges: *H. albocristata* Gosliner & Fahey, 1998, *H. xishaensis, H. dalanghita*. All others have orange or yellow ridges, while the outgroup taxon has the same coloration over its entire dorsum. Ridges that are the same color as the dorsum is considered the plesiomorphic state and differently colored ridges are considered as unordered apomorphies.

8. Dark marginal lines.—Dark marginal lines are unique to four *Halgerda*: *H. albocristata, H. elegans* Bergh, 1905, *H. iota* Yonow, 1993 and *H. willeyi* Eliot, 1903. The marginal lines lie perpendicular to the mantle edge. These marginal lines are not present on the outgroup taxon. Lack of marginal lines is the plesiomorphic state.

9. Dark spots.—Dark dorsal spots are present on five *Halgerda*: *H. brunneomaculata, H. formosa, H. punctata, H. dalanghita* and *H. maricola*. These spots can range from deep purple-black to dark brown. The outgroup taxon does not have these distinguishing spots, and this state is plesiomorphic.

10. Gill branching.—Only *H. dalanghita* shares the tripinnate gill branching pattern with the outgroup taxon *Asteronotus*. The tripinnate gill pattern is considered plesiomorphic.

11. Gill spots.—Dark spots on the gill branches are considered the apomorphic state. Seven species have these symmetrical round spots. The other *Halgerda* species lack spots and share the plesiomorphic state with the outgroup taxon.

12. Gill stripes.—Lack of dark gill stripes is the plesiomorphic state, and 14 species share this state with the outgroups. Thirteen species have dark stripes on the gill branches. The stripes run from bottom to top, along the posterior of the gill rachis.

13. Gill tips.—All but four *Halgerda* species share the plesiomorphic character with the outgroup taxon with white gill tips that are the same color as the rest of the gill. The four *Halgerda* that have black gill tips are: *H. albocristata, H. elegans, H. formosa*, and *H. toliara*.

14. Gill shape.—Only three *Halgerda* species have gill branchia that lie flat on the dorsum: *H. punctata, H. dalanghita*, and *H. gunnessi*. All other species including the outgroup taxon have erect gill branchia. This is considered the plesiomorphic state.

15. Gill pinnation.—The plesiomorphic character state is a highly pinnate gill. This state is shared by the outgroup taxon and *H. dalanghita*. All other *Halgerda* have a moderately pinnate gill except for *H. brunneomaculata* and *H. toliara* which have a sparsely pinnate gill.

16. Rhinophore base color.—The rhinophoral base is the same as the body color in *Asteronotus*. Four *Halgerda* species share this plesiomorphic character state: *H. albocristata, H. elegans*, and *H. toliara* and *H. maricola*. The three other character states: black blotches, black spots and black stripes are distributed equally among the other *Halgerda* species. This character is treated as unordered.

17. Rhinophoral pigment.—Randomly placed dark pigment is the plesiomorphic state. Six *Halgerda* species have speckled pigment on the rhinophores: *H. aurantiomaculata, H. carlsoni, H. malesso, H. terramtuentis, H. batangas* and *H. diaphana*.

18. Rhinophore bulb.—A rhinophoral bulb that is the same color as the body is the plesiomorphic state, and this state is only present in *Asteronotus*. All *Halgerda* species have black coloration on the bulb.

19. Gill glands.—All *Halgerda* share the apomorphic character state of opaque white glands internal to the gills. This character state could not be determined for *H. xishaensis* based on the original description. The outgroup taxon has gill glands that are not opaque.

20. (Oral tentacles.—Short rounded oral tentacles were considered plesiomorphic. Half of the *Halgerda* species share this character state with the outgroup taxon. The character state could not be determined from the literature for *H. iota*. This character was omitted from the analysis because the shape of the oral tentacles was found to vary intraspecifically according to fixation artifacts).

21. Foot border.— *Asteronotus* does not have a colored margin around the foot. Thirteen *Halgerda* species have a yellow or orange foot margin. This character state could not be determined for *H. dalanghita*. Lack of a foot margin is considered plesiomorphic.

22. Foot lines.—Dark colored foot lines are absent in the outgroup taxa, and in most *Halgerda* species. However, *H. iota, H. tessellata* and *H. willeyi* have dark lines along the edge of the foot. Dark lines on the foot is considered apomorphic.

23. Foot spots.—Nearly half of the *Halgerda* species have dark spots on the foot. *Asteronotus*, the outgroup, and the other half of the *Halgerda* species do not have dark foot spots. This is considered the plesiomorphic state.

24. Body shape.— *Asteronotus* has a broad body shape; the plesiomorphic state. This shape is shared by half the *Halgerda* species. The other half have a more elongate body shape.

25. Secondary orange lines.—Nine *Halgerda* species have secondary orange lines on the notum between the ridges. *Asteronotus* does not have these secondary lines, and this is considered the plesiomorphic state.

26. Orange dots.—Orange dots on the notum is the apomorphic character state of three *Halgerda* species: *H. aurantiomaculata, H. carlsoni* and *H. bacalusia*. The outgroup taxon and the remaining *Halgerda* do not have orange dots on the notum.

27. Radula sac.—The radular sac of most *Halgerda* is elongate. Only *H. dalanghita* has a short radular sac, which is the plesiomorphic character state of the outgroup taxon *Asteronotus*. The character state could not be determined for five taxa.

28. (Teeth rows.—Eleven *Halgerda* species share the plesiomorphic state of inner lateral teeth aligned in straight rows.

Datamatrixws	1 rhino	2 ridge	3 tube	4 sma	5 cary	6 body	7 ridge	8 black	9 black	10 gill t	11 gill s	12 gill	13 gill	14 gill s	15 gill p	16 rhino	17 rhino	18 rhino	19 gill g	20 oral	21 foot	22 foot	23 foot	24 body	25 secc	26 aran	27 radu	28 teeth	29 bucc	30 radu	31 mid	32 aute	33 aute	34 fimb	35 amp	36 vagin	37 vagin	38 vagin	39 vagin	40 vagin	41 pros	42 diffe	43 ejac	44 rece	45 tube	46 penis	47 uteri	48 pros	49 atriu	50 man
1 albacristrata	1	1	2	0	1	1	2	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0
2 aurantiomaculata	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	1	1	0	1	1	0	1	1	1	0	0	1	1	1
3 brunneomaculata	1	1	0	1	1	0	1	0	1	1	0	1	0	0	2	3	0	1	1	1	0	0	1	1	0	0	?	1	0	1	0	1	0	1	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	2
4 carlsani	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	0	1	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	1	0	1	1	0	0	0	0	0
5 elegans	1	1	2	0	1	1	1	1	0	1	0	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	1	2	1	0	1	1	0	0	1	1	0	1	1	0	0	0	1	0	0	0
6 formosa	1	1	0	1	1	1	1	0	1	1	0	0	1	0	1	1	0	1	1	1	1	0	1	1	0	0	1	1	1	1	1	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	0	0
7 graphica	1	1	2	0	1	1	1	0	0	1	0	1	0	0	1	3	0	1	1	0	0	0	1	0	1	0	?	1	?	1	0	0	0	?	?	?	?	?	?	?	1	?	?	0	?	?	?	0	?	0
8 guahan	1	1	0	0	1	1	1	0	0	1	0	0	0	0	1	3	0	1	1	0	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0
9 iota	1	1	0	0	1	1	1	1	0	1	0	1	0	0	1	3	0	1	1	?	0	1	1	0	0	0	?	0	?	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
10 malessa	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	1	1	0	0	0	1	0	?	0	0	1	0	1	0	0	0	1	1	0	1	0	1	1	1	0	1	0	0	0	1	1
11 punctata	1	1	1	0	1	1	1	0	1	1	0	1	0	1	1	3	0	1	1	0	0	0	1	1	0	0	1	1	0	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
12 terramtuentis	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	0	1	0	0	0	1	0	1	0	?	1	0	1	0	0	0	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0
13 tessellata	1	1	2	1	1	1	1	0	0	1	0	1	0	0	1	3	0	1	1	1	0	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	1
14 wasinensis	1	1	2	0	1	1	1	0	0	1	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0
15 willeyi	1	1	0	0	1	1	1	1	0	1	0	1	0	0	1	3	0	1	1	1	0	1	1	0	0	0	1	0	1	1	0	0	0	?	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0
16 xishaensis	1	1	0	0	1	0	2	0	0	1	0	0	0	0	1	?	0	1	?	0	0	0	0	0	0	0	?	?	?	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
17 dalanghita	1	1	2	0	1	0	2	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	1	?	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0
18 batangas	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	0	1	1	1	0	1	0	0	1	1	0
19 stricklandi	1	1	1	0	1	1	1	0	0	1	0	1	0	0	1	3	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	0
20 bacalusia	1	1	1	0	1	1	1	0	0	1	0	1	0	0	1	3	0	1	1	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	1
21 dichramis	1	1	0	0	1	1	1	0	1	1	0	1	0	1	1	1	0	1	1	1	?	?	?	1	0	0	1	1	?	1	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0
22 toliara	1	1	0	1	1	0	1	0	0	1	0	0	1	0	2	0	0	1	1	1	0	0	0	1	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	2
23 diaphana	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	1	1	1	0	1	0	0	0	1	0	1	1	0	1	0	?	0	?	0	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1
24 asteranatus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25 gunnessi	1	1	0	0	1	1	1	0	0	1	0	1	0	1	1	3	0	1	1	1	1	0	1	1	0	0	1	1	0	1	0	1	0	?	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1
26 theabroma	1	1	0	0	1	1	1	0	0	1	0	1	0	0	1	3	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	1	0	0	?	1	1	1	0	1	0	1	1	1	0	1	0	1	1	0	1
27 brycei	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	2	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1	1	0	0
28 maricola	1	1	0	0	1	1	1	0	1	1	0	0	0	0	1	0	0	1	1	1	1	0	0	1	0	0	1	1	0	1	0	1	0	0	0	?	1	1	1	0	1	0	1	1	1	0	1	0	1	0	1
29 paliensis	1	1	2	0	1	0	1	1	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2

The other species teeth are arranged in a V-shaped pattern. This character was omitted from the analysis when it was found that the two conditions intergraded in some species).

29. Buccal mass.—Most *Halgerda* species have an unpigmented buccal mass as does *Asteronotus*. However, *H. albocristata*, *H. formosa*, *H. wasinensis* Eliot, 1903 and *H. willeyi* all have dark pigmentation on the buccal mass. An unpigmented buccal mass is the plesiomorphic state. This character state could not be determined for *H. graphica* Basedow & Hedley, 1905, *H. iota*, *H. xishaensis* or *H. dalanghita*.

30. Radula shape.—The shape of the radular ribbon is nearly square in *Asteronotus* and *H. dalanghita*. This radula shape is the plesiomorphic state. All other *Halgerda* species have a rectangular radular ribbon.

31. Middle lateral teeth.—All *Halgerda* except *H. dalanghita* share the plesiomorphic character state of hamate middle lateral teeth. *H. dalanghita* has elongate middle lateral teeth.

32. Outer lateral teeth shape.—Pointed, undivided outer lateral teeth is the plesiomorphic character state which is shared by *Asteronotus*, *H. graphica*, *H. iota*, *H. willeyi*, *H. dalanghita*, *H. gunnessi*, *H. theobroma and H. maricola*. The remaining *Halgerda* species have fimbriate outer lateral teeth.

33. Outer lateral teeth size.—Only *H. dalanghita* has outer lateral teeth that are the same size as the middle lateral teeth. *Asteronotus* and all other *Halgerda* species have smaller outer lateral teeth than the middle teeth. The presence of smaller outer lateral teeth is the plesiomorphic state and the teeth of *H. dalanghita* are autapomorphic.

34. Fimbriate teeth.—Of the species that have fimbriate outer teeth, only *H. albocristata*, *H. brunneomaculata* and *H. elegans* have elongate fimbriate teeth. All other species have short fimbriate teeth. This character state was not applicable to the eight species that lack fimbriate outer teeth. The presence of short fimbriate outer lateral teeth is considered the plesiomorphic character state.

35. Ampulla length.—A long ampulla is considered plesiomorphic. This character state is shared by both outgroup taxa and most *Halgerda* species. Eight *Halgerda* have a short ampulla. Data was unavailable for four species: *H. graphica*, *H. iota*, *H. punctata* and *H. xishaensis*.

36. Vaginal duct length.—Fourteen *Halgerda* species share the plesiomorphic character state of an elongate vaginal duct with *Asteronotus*. All other *Halgerda* have an short vaginal duct. Data were unavailable for the same four species as in character 35.

37. Vagina shape.—The outgroup taxon and most *Halgerda* species have a narrow vagina. Six *Halgerda* have a wide vagina: *H. malesso*, *H. terramtuentis*, *H. batangas*, *H. diaphana*, *H. theobroma* and *H. maricola*. A narrow vagina is the plesiomorphic character state.

38. Vagina duct.—The vaginal duct enters a common atrium in the outgroup taxon and in all *Halgerda* except *H. albocristata*, *H. aurantiomaculata*, *H. elegans*, *H. guahan* and *H. willeyi*. Data were unavailable for the same four species noted in character #35. A common atrium is the plesiomorphic state.

39. Vaginal base.—A narrow vaginal base is considered the plesiomorphic character state. Three *Halgerda* share this state with the outgroup taxon: *H. brunneomaculata*, *H. dalanghita* and *H. toliara*. No data are available for the four *Halgerda*

species mentioned in character #35.

40. Vaginal sphincter.—A sphincter at the top of the vagina is present in six *Halgerda* species: *H. formosa, H. tessellata, H. wasinensis* Eliot, 1903, *H. willeyi, H. dalanghita* and *H. gunnessi*. No sphincter is present in the outgroup taxon, and this is considered the plesiomorphic state. No data are available for the same four *Halgerda* species as in character #35.

41. (Prostate.— All *Halgerda* and *Asteronotus* studied have a two-part prostate. Data were unavailable for the same four species as noted above. This character was omitted from the analysis due to all species sharing the same character state).

42. (Differentiation of prostate.—All taxa studied except *H. dalanghita* have a well differentiated prostate. *Asteronotus* and *H. dalanghita* have a poorly differentiated prostate. A poorly differentiated prostate is the plesiomorphic state. Data were missing for the same four species noted above. This character was omitted from the analysis due to its similarity to character #41).

43. Ejaculatory duct.—An elongate ejaculatory duct is the plesiomorphic character state, and the outgroup taxon shares this state with half the *Halgerda* species. The ejaculatory duct is short in all other *Halgerda* for which data were available.

44. Receptaculum seminis.—The receptaculum seminis is substantially smaller than the bursa copulatrix in the outgroup taxon and in all *Halgerda* species except *H. brunneomaculata* and *H. carlsoni*. In those two species, the receptaculum is the same size as the bursa.

45. Tubercular vaginal glands.—Tubercular vaginal glands are present in 11 *Halgerda* species. This is considered apomorphic. Lack of tubercular vaginal glands is the character state shared by the outgroup taxon and the remaining *Halgerda* species for which data were available.

46. Penis.—Three *Halgerda* species have a tubular penis: *H. brunneomaculata, H. formosa* and *H. dalanghita*. All other *Halgerda* for which data were available have a bulbous penis like *Asteronotus*. A bulbous penis is the plesiomorphic state.

47. Uterine duct insertion.—The uterine duct inserts at the base of the bursa in the outgroup taxon, and in most *Halgerda* species. In six *Halgerda* species, the duct inserts at a point more distal to the bursa, closer to the base of the receptaculum seminis. This is considered apomorphic. No data were available for the same four *Halgerda* species.

48. (Prostate.—The prostate is smaller than the female gland mass in the outgroup taxon and in half the *Halgerda* species. In the other half, the prostate is the same size as the female gland mass. No data were available for the same four species. The smaller prostate is considered plesiomorphic. This character was omitted from the analysis because individuals vary according to differing degrees of reproductive maturity).

49. Atrium pigment.—Dark pigmentation is present on the genital atrium of six *Halgerda* species. All other species, including the outgroup taxon have no pigmentation on the genital atrium. This is the plesiomorphic state.

50. Mantle margin.—A colored margin around the perimeter of the mantle is a character state shared by ten *Halgerda* species. The outgroup taxon does not have a colored mantle margin. Lack of a colored mantle margin is considered plesiomorphic.

RESULTS AND DISCUSSION

In order to develop phylogenetic hypotheses regarding *Halgerda*, the above described characters were placed into a data matrix (Table 2) from MacClade version 3.04 (Maddison & Maddison, 1998). All characters used have equal weight and are unordered. Five characters were deleted from the first analysis due to being parsimoniously uninformative. The characters deleted from further analyses are indicated in parentheses in the character descriptions (previous section). The data were analyzed by Phylogenetic Analysis Using Parsimony (PAUP) version 4.0b2 by David Swofford (1999). A heuristic search was performed with the optimality criterion of maximum parsimony. The stepwise addition option of Random Trees was used, with 100 repetitions, starting from random start trees. Six most parsimonious trees were produced. The trees required 123 steps and had a consistency index of 0.415 and a retention index of 0.585. The strict consensus tree is shown in Figure 9. Figure 10 shows the majority rule tree with the character numbers and character reversals. The underlined numbers indicate reversals.

An evaluation was performed of one million trees sampled randomly from the set of all possible trees. The mean of that evaluation is 224.607, the standard deviation is 8.311, the g1 statistic is –0.407 and the g2 statistic is 0.152.

A decay analysis was performed using a heuristic search by PAUP for all trees $\leq$124 steps. A 50% majority-rule consensus of 518 trees was computed. The CI is 0.411 for this tree.

Character analysis indicates that nearly half of the characters were subject to at least one instance of homoplasy, either parallelism or reversal. Figure 10 shows those characters by number. Some of these characters are: small marginal tubercles, elongate, fimbriate outer teeth, penis shape, ejaculatory duct length, vaginal duct shape and length, and the uterine duct insertion point. Nine homoplastic characters relate to color.

Several apomorphies exhibit no instance of parallelism or reversal. They include: a wide vagina base, a vaginal sphincter, a tubercular vaginal gland, a bipinnate gill, erect gill branchia, an elongate radular sac, dorsal ridge color that is different from the body color and visible gill glands.

Further character analysis and testing of the data will be performed to strengthen the phylogenetic hypothesis of the genus *Halgerda*.

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Food availability and trophic needs of *Peltodoris atromaculata* (Mollusca: Doridacea)

Riccardo Cattaneo-Vietti, Stefano Schiaparelli & Mariachiara Chiantore

KEY WORDS: *Peltodoris atromaculata*, trophic activity, energy balance.

ABSTRACT *Peltodoris atromaculata* (Bergh, 1880), a Mediterranean doridacean mollusc (Nudibranchia: Doridacea) very common in the pre-coralligenous and coralligenous communities, feeds almost exclusively upon *Petrosia ficiformis*, a diffuse demosponge hosting, in its symbiocortex, a dense cyanobacteria population. Considering its strong monophagy, this mollusc seems to be adequate for studying energy fluxes between benthic filter-feeders and carnivores and for verifying trophic needs and energy balance in a monophagous predator. Laboratory experiments (trophic activity, calorimetry) and *in situ* observations have allowed to evaluate the trophic activity of this species (a 30 mm long mollusc grazes, daily, a surface of about 50 mm² of *Petrosia*) and to calculate average energetic value of its prey (symbiocortex: 6335.4 cal/g AFDW; medulla: 6219.0 cal/g AFDW). As the water content of the sponge is about 73 % and its ash content is about 15 % of WW, the edible organic matter is about 11-12 % of the whole sponge tissue. Considering these values, the energetic value of 1 mm3 of *Petrosia* (being its specific weight 1.2 0.11 g/mm3) is 0.9 cal. During the whole life cycle (24 months) of *Peltodoris*, considering that it can reach a maximum length of 100 mm, it needs about 500 cm2 of *Petrosia*, (equivalent to 46000 cal), of which about 14000 are lost as heat.

RIASSUNTO *Peltodoris atromaculata* (Bergh, 1880), mollusco doridaceo (Nudibranchia: Doridacea), molto comune nelle comunità mediterranee del coralligeno e pre-coralligeno, si nutre in modo quasi esclusivo di *Petrosia ficiformis*, una demospongia assai diffusa che ospita, nella propria symbiocortex, una densa popolazione di cianobatteri. Grazie alla sua stretta monofagia, questo mollusco sembra adeguato per effettuare studi sui flussi energetici tra organismi bentonici sospensivori e carnivori e per analizzare le necessità trofiche ed il bilancio energetico in un predatore monofago. Esperimenti condotti in laboratorio (attività alimentare, calorimetria) ed osservazioni effettuate *in situ* hanno permesso di valutare l'attività trofica di questa specie (un individuo lungo 30 mm si nutre, quotidianamente, di una superficie di circa 50 mm² di *Petrosia*) e di calcolare il valore energetico medio della sua preda (symbiocortex: 6335.4 cal/g AFDW; medulla: 6219.0 cal/g AFDW). Dal momento che il contenuto in acqua della spugna si aggira intorno al 73 % e quello delle ceneri è pari a circa il 15 % del WW, la frazione organica edule è pari a circa l'11-12 % del peso totale della spugna. Considerando tali valori, il valore energetico di 1 mm3 di *Petrosia* (il cui peso specifico è 1.2 0.11 g/ mm3) è pari a 0.9 cal. Durante l'intero ciclo vitale di *Peltodoris* (24 mesi), considerando che può raggiungere una lunghezza massima di 100 mm, questo nudibranco necessita di circa 500 cm2 di *Petrosia* (equivalenti a 46000 cal), delle quali circa 14000 sono consumate nella respirazione.

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INTRODUCTION

Nudibranch molluscs are considered stenophagous predators (Todd, 1981), but indeed just few species show a real monophagy, as generally the predator chooses on a bulk of preys, often taxonomically allied. This could bias the evaluation of the trophic needs of a supposed monophagous species, being the food availability wider and diversified than supposed.

Differently, *Peltodoris atromaculata* Bergh 1880, a Mediterranean doridacean mollusc (Nudibranchia: Doridacea), very common in the pre-coralligenous and coralligenous communities (Haefelfinger, 1961; Avila, 1996), feeds almost exclusively upon *Petrosia ficiformis* (Poiret, 1789), a widespread Mediterranean demosponge, hosting in its cortex a dense cyanobacteria population, belonging to the species *Aphanocapsa feldmanni* (Sarà & Liaci, 1964; Sarà *et al.*, 1998). Rarely, young specimens of *Peltodoris* were observed to feed on the sponge *Reniera fulva* Topsent, 1893 (Cattaneo-Vietti *et al.*, 1993).

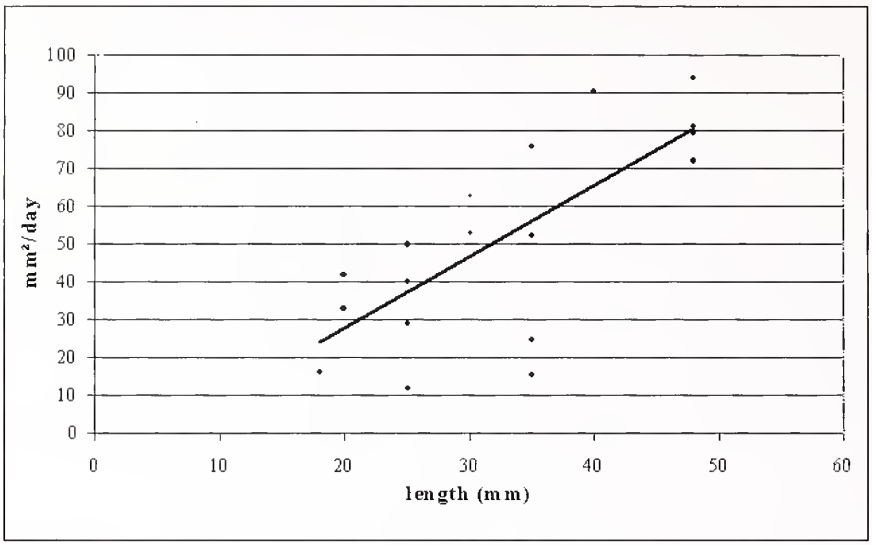
Behavioural tests and biochemical analyses have underlined its feeding preference: Castiello *et al.* (1980) showed the ability of the mollusc to absorb and retain high molecular weight polyacetylenes (petroformynes) from its prey, often showing a strong cytotoxic effect and used as bioactive chemicals against predation.

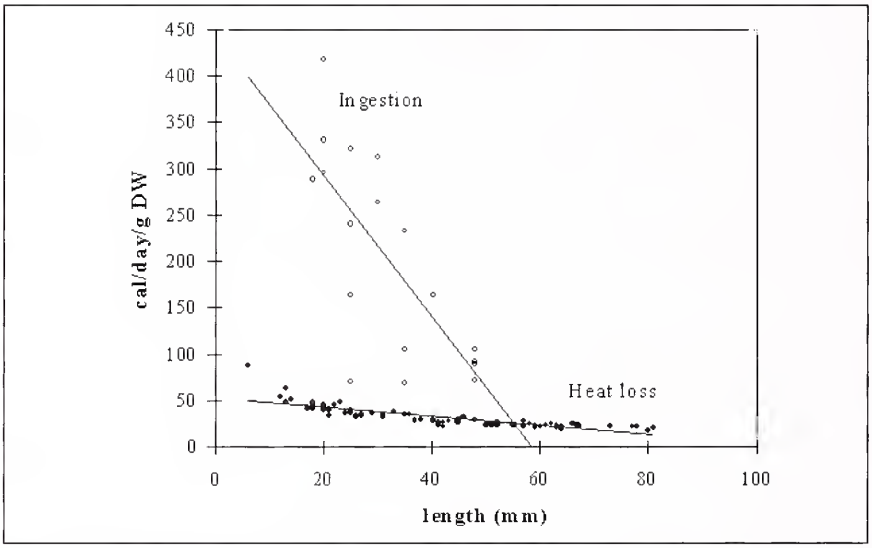
Consequently, considering the strong monophagy of this mollusc, the *Peltodoris* vs *Petrosia* predation model seems to be adequate for studying energy fluxes between benthic filter-feeders (the sponge) and carnivores (the mollusc). Moreover, it could be useful to evaluate the trophic needs and the energy balance in a marine monophagous predator.

MATERIAL AND METHODS

In order to measure the amount of sponge daily eaten, 16 specimens of *Peltodoris atromaculata* (20 to 80 mm in length) were collected from several stations placed along the Portofino Promontory (Ligurian Sea) between February and September 1997. Nudibranchs were taken to the laboratory and placed in holding chambers (1 litre plastic containers with screened sides to allow water circulation) inside aquaria with flowing, filtered sea-water at ambient temperature (16° C). In each container a specimen of *Petrosia ficiformis*, collected in the same site, was placed. Every week, sponges were substituted and the eaten surface was measured using a *camera lucida* connected with a PC.

In order to evaluate the energetic content of *Petrosia* and *Peltodoris*, additional 8 specimens were collected, at different depths, in April and December 1997. The calotific content of





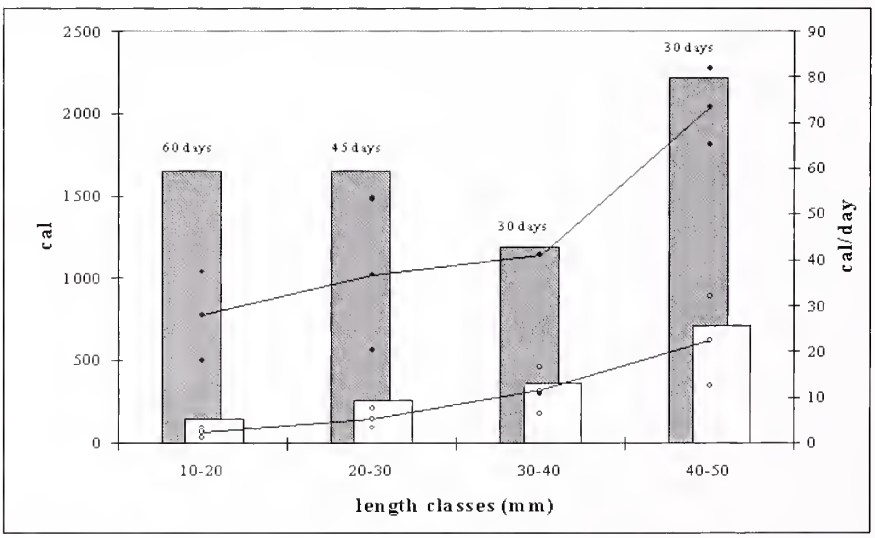


Fig. 1: Daily eaten surface of the sponge *Petrosia ficiformis* by different sized *Peltodoris atromaculata*. Fitting linear correlation: Y = 1.89 X –10.29; R≤ = 0.56; df = 16; p < 0.001.

Fig. 2: Weight specific daily ingestion and heat loss rates in different sized *Peltodoris atromaculata*. Ingestion: Y = -7.61 X + 444.81; R≤ = 0.54; df = 16; p < 0.001. Heat loss: Y = -0.51 X + 53.06; R≤ = 0,71; df = 79; p < 0.001.

Fig. 3: Total ingestion (grey histograms) and heat loss (white histograms) in calories by *Peltodoris atromaculata* growing from each size class to the next one (days spent reported on top of histograms). Daily ingestion (black dots) and daily heat loss (white dots), reported in the linear graphics (avg ± std).

Table 1 *Petrosia ficiformis:* Calorific content (cal/g AFDW) of cortex and medulla (avg ± std) and chl-*a* content of the cortex (mg/cm2) measured in specimens collected at different depths

Depth (m)	Cortex (n = 8)	Medulla (n = 8)	chl-*a* content
5	6609.8 ± 452.2	6484.0 ± 359.9	42
10	6184.1 ± 789.7	6101.4 ± 656.0	30
20	6244.9 ± 697.3	5781.0 ± 361.7	31
30	6278.1 ± 568.8	6762.9 ± 362.6	17
40	6665.5 ± 505.0	6798.1 ± 363.1	4
50	6138.4 ± 328.2	6004.6 ± 323.1	
Cave	6227.2 ± 266.4	5601.2 ± 137.4	
Avg	6335.4 ± 515.4	6219.0 ± 471.7	

Table 2 Energetic content and ash % in different mollusc species. All data, except present data for *Peltodoris atromaculata*, are from PAINE, 1964

Species	Ash DW %	cal/g AFDW
Peltodoris atromaculata	34	5644
Aegires albopunctatus	43	5309
Polycera atra	28	5680
Triopha maculata	27	5641
Acanthodoris rhodoceras	41	5439
Hopkinsia rosacea	43	6007
Dendrodoris albopunctata	40	5158
Dirona picta	41	6675
Flabellina iodinea	30	4943
Hermissenda crassicornis	28	6446
Bulla gouldiana (without shell)	25	6352
Haminoea virescens (without shell)	27	5335
Navanax inermis	36	5992
Aglaja diomedea	27	5555

these specimens was estimated using a Phillipson microbomb: samples were washed, dry frozen and sifted to obtain a powder as fine as possible, prepared as pellets (0.02 g DW) and burned (PHILLIPSON, 1964; PRUS, 1975). A known amount of benzoic acid was added to the pellets to act as a binding agent and used as a standard. Ash weight (ADW) percent content of sponge and mollusc tissues was obtained by placing dried samples in a muffle at 500C for 4 h. The edible matter percent of *Petrosia* was estimated considering the ratio between the AFDW (DW-ADW) and the total WW.

The estimation of the basal metabolism of *Peltodoris* was performed using the formula proposed by CRISP (1971):

Q (cal/day) = A wb

where:
A = 1.05
b = 0.8
w = g DW
at T = 15° C

RESULTS

The energetic content of the tissues of the mollusc, measured as cal/g AFDW in 8 specimens, is 4786 ± 227 in the foot, 5687 ± 579 in the mantle 6458 ± 241 in the viscera, without significant differences. The average ash content of mollusc tissues is about 33.9 9.3 %. The foot and the mantle show quite similar values (39.5 ± 3.8 % and 39.3 ± 1.0 % respectively), while vis-

cera show a lower value (19.3 ± 0.2 %), due to the absence of calcareous spicules in these tissues (CATTANEO-VIETTI *et al.*, 1993, 1995).

The data on the energetic content of the symbiocortex and the medulla of *Petrosia ficiformis* collected at two different depths are reported in Table. 1. The average energetic value of the symbiocortex is 6335.4 cal/g AFDW, while that of the medulla is 6219.0 cal/g AFDW. The water and ash content percentages are 73.5 4.5 % and 14.7 3.5 %, respectively. Consequently the edible organic matter is 11.74 %. Considering these values and its specific weight (1.2 0.11 g/cm3), the energetic value of 1 mm3 of *Petrosia* is 0.9 cal.

Figure 1 shows the trends of the trophic activity of *Peltodoris* in aquaria, on the basis of the daily grazed surface by each specimen. The depth of this area is about 1 mm. On average, a specimen of middle size (30 mm long) grazes, daily, a surface of about 50 mm^2 of *Petrosia*.

The weight specific eaten surface, calculated as cal/day/g is, obviously, higher in smaller specimens, which consume, as DW, three times more sponge tissues than larger ones, while the weight specific heat loss does not vary significant according to the mollusc size (Fig. 2).

The global energy balance of *Peltodoris atromaculata*, in accordance with the growth rate proposed by AVILA (1996), has been summarised in Figure 3. During 165 days, the time needed to reach a length of 40-50 mm, this mollusc grazes about 74 cm2 of *Petrosia*, corresponding to 6700 cal and consumes about 1475 cal as heat loss.

DISCUSSION AND CONCLUSIONS

From an energetically point of view, the study of the trophic relationship between the nudibranch *Peltodoris atromaculata* and its prey, the sponge *Petrosia ficiformis*, has allowed to evaluate the trophic needs and the energy balance of the mollusc.

In *P. atromaculata*, the energetic contents of the mantle and the foot are similar, even if the mantle one is lightly higher, because of the presence of insoluble proteins due to a larger amount of connective tissue. The viscera show, as expected, the highest values, due to the high lipid contents in the hepatopancreas and reproductive systems. The energetic content of the mollusc is in accordance with the values reported by PAINE (1964) as shown in Table 2. The calorific value of the sponge seems to be independent from its symbiotic fraction. In fact, although the cyanobacteria population, measured as chl-*a* values, reduces progressively with depth (BAVESTRELLO *et al.*, 1994), the calorific values remain relatively constant. Moreover, very little differences are found between symbiocortex and medulla at all depths, conforming the low contribute of the symbionts to the global energetic value of the sponge.

During the whole life cycle of *P. atromaculata* (24 months), considering that it can reach a maximum length of 100 mm and assuming a constant daily ingestion rate in individual between 50 and 100 mm in length, it needs about 500 cm2 of *Petrosia*, equivalent to 46000 cal, about 14000 of which lost as heat. This amount fits with a sponge of 20-24 cm of diameter. It follows that one specimen of this nudibranch needs a middle size *Petrosia* for its subsistence during the whole life cycle.

The frequency of *Petrosia* in the Mediterranean hard bottom communities and its ability to regenerate the simbiocortex, avoiding necrosis, suggest that the food requirement is not a constraint for *P. atromaculata* population. Since this mollusc seems to have strong chemical defensive systems (CIMINO *et al.*, 1980, 1983; AVILA, 1995) and no specific predator is known, its density must be controlled by other factors, probably during the larval life, where predation may be intense even if not selective.

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Review of reproduction in the Sacoglossa (Mollusca, Opisthobranchia)

Kathe R. Jensen

KEY WORDS: Sacoglossa, Opisthobranchia, reproductive systems, development patterns, fecundity, distribution.

ABSTRACT A brief summary of functional morphology of reproductive systems in the Sacoglossa is given. Penial morphology appears to have been important in speciation. Loss of penial armature has apparently occurred repeatedly in sacoglossan evolution; it may be a single gene mutation and may serve as a rapid means of reproductive isolation. Extracapsulat yolk (ECY) occuts only in the superfamily Plakobranchoidea. Its function and origin are still debated. Reproductive data fot 98 species of Sacoglossa are summarized. The correlation between relative capsule size and development type is confirmed. Development pattern is not related to phylogeny, neither at family nor genus level. The fraction of species with non-planktotrophic development appears to be higher in the Caribbean than in any other zoogeographic tegions. This is interpreted as an example of local (sympatric) speciation. Cladistic analysis may help to resolve this. Information on mating and spawning behaviour is scarce, as is information on aspects of fertilization. The existing information is summarized and its phylogenetic and evolutionary importance discussed.

RIASSUNTO Viene qui presentata una breve revisione della morfologia funzionale del sistema riproduttivo dei Sacoglossa. La morfologia del pene è un elemento importante nella speciazione: la perdita dell'armatura sembra essere avvenuta ripetutamente nel corso dell'evoluzione del gruppo, probabilmente causata dalla mutazione di un singolo gene e potrebbe essere stata alla base di un rapido isolamento riproduttivo. Il tuorlo extracapsulare (ECY) è presente solo nella superfamiglia Plakobranchoidea e la sua funzione ed origine sono ancora incerte. Vengono qui presentati i dati relativi all'attività riproduttiva di 98 specie di Sacoglossa. Il rapporto tra taglia della capsula e tipo di sviluppo viene confermato. Le caratteristiche dello sviluppo non sono collegate nè alla filogenesi, nè sono omogenee a livello di famiglia o genere. Il gruppo di specie a sviluppo non planctotrofico appare più comune nel Mare Caraibico che in qualsiasi altra area zoogeografica e può essere interpretato come un esempio di speciazione simpatrica. L'analisi cladistica potrebbe aiutare a comprendere questa anomalia.
Dati relativi all'accoppiamento e alle tecniche di deposizione sono ancota pochi, tanto quanto quelli relativi alla fertilizzazione. I dati esistenti vengono qui sintetizzati e discussa la loro importanza filogenetica ed evolutiva.

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INTRODUCTION

Sacoglossan opisthobranchs are simultaneous hermaphrodites requiring copulation for transfer of allosperm for internal fertilization. Reproductive systems are highly complex and the function is incompletely understood (JENSEN, 1997b). Data on egg size and development type for Caribbean sacoglossans were reviewed by CLARK & JENSEN (1981). Since then data for a large number of species from other regions have been published. Sacoglossans differ from most other opisthobranchs in that egg size is not a good indicator of development type (CLARK & JENSEN, 1981; DEFREESE & CLARK, 1983; HADFIELD & MILLER, 1987). Instead the relative size of egg capsules may be a more reliable indicator of development type (CLARK & JENSEN, 1981). Sacoglossan egg masses are gelatinous clusters, more or less cylindrical, and coiled into more or less regular spirals (CLARK *et al.*, 1979; HADFIELD & SWITZER-DUNLAP, 1984; JENSEN, 1992, 1997a). The eggs are usually encapsulated singly, though twin embryos are seen in a number of species (JENSEN, 1992). A peculiar feature of many sacoglossan egg masses is the occurrence of extracapsular yolk (CLARK *et al.*, 1979; BOUCHER, 1983). The function of this is still not clear, but it may be nutritional in some species, defensive in others.

Three developmental patterns are usually distinguished in opisthobranchs (THOMPSON, 1967). Planktotrophic larvae have a long pelagic phase during which they feed. Lecithotrophic larvae have a short swimming phase, lasting from several hours to a few days, during which no feeding takes place; the pelagic phase may be extended and feeding initiated if a suitable substrate is not located in a few days (KEMPF & TODD, 1989). In species with direct development fully formed juveniles hatch from the egg mass. In most opisthobranchs, including the Sacoglossa, a veliger stage is actually formed within the egg capsule, but metamorphosis is completed prior to hatching (CLARK *et al.*, 1979; CLARK & JENSEN, 1981; JENSEN, 1997b). It is generally assumed that the incidence of direct development increases with latitude; this is known as Thorson's rule, and it has been claimed that this rule does not apply to the Sacoglossa (CLARK & GOETZFRIED, 1978).

In the present study reproductive anatomy of the Sacoglossa is summarized, and data on egg size, capsule size and development type are reviewed. This is correlated with phylogeny, latitudinal and regional distribution. Other aspects of reproductive biology, such as mating behaviour and fecundity, are also discussed.

MATERIALS AND METHODS

Most data have been taken from information scattered in the taxonomic literature. Some unpublished observations made during international marine biological workshops in Hong Kong and Western Australia are also included. The sources of the data, including authorship for species, are shown in Appendix 1.

Measurements of egg diameters are for uncleaved eggs, and measurements of capsule size in most cases include the longest diameter, and a short diameter perpendicular to this (Fig. 1). In cases where ranges have been given, the median value has been used in calculations.

Table 1. Data on egg diameter and development type in relation to geographical latitude of shelled Sacoglossa (Oxynoacea).

Taxon	Latitude	Egg diam.	Dev. type
Family Volvatellidae			
Ascobulla			
fischeri	35S	?	P
A. ulla	25N	60µm	ED
Volvatella			
australis	25S	100.8±6.2µm	L?
V. bermudae	32N	66µm	P
V. ventricosa	35S	97.2±10.5µm	P?
Family Juliidae			
Julia japonica	30-35N	65µm	P
Berthelinia			
australis	38S	54µm	P?
B. caribbea	25N	100µm	L
B. darwini	25S	102.8±5.9µm	L?
B. ganapati	10-20N	50µm	P
B. limax	30-35N	250µm	L
B. rottnesti	35S	?	L?
Family Oxynoidae			
Oxynoe			
antillarum	25N	63µm	P
O. azuropunctata	25N	120µm	L
O. olivacea	40N	62-69µm	P
Same	28N	250µm	?
O. panamensis	10N	?	P
O. viridis	25S	72µm	P
Same	35S	56µm	P
Lobiger			
sagamiensis	22N	?	P?
L. souverbiei	25N	56µm	P

Abbreviations: ED, encapsulated direct; L, lecithotrophic; P, planktotrophic

RESULTS

Review of reproductive systems (from JENSEN, 1996, 1997b): The sacoglossan gonad is hermaphroditic, though a few species have separate male and female follicles. Gamete formation has not been studied, and ultrastructure of spermatozoa has only been described in one species (HEALY, 1993). Oocytes usually mature after spermatocytes, so animals may copulate as males before they are able to spawn. The genital system is either androdiaulic or triaulic; that is, there is a vas deferens separated from the female system, which again may have a separate route for transporting allosperm. The hermaphroditic duct usually forms an ampulla where autosperm is stored. The male system consists of an internal closed vas deferens, a prostate gland, and an eversible penis enclosed in a penial sheath. The prostate is a glandular part of the vas deferens in the shelled Oxynoacea, but a separate gland opening into the vas deferens in the non-shelled Plakobranchacea. In the cerata-bearing Limapontioidea the prostate is composed of a number of short lobes; in the parapodia-bearing Plakobranchidae it is highly branched throughout the visceral mass. The function of the prostatic secretion is unknown. At least 3 possibilities exist: (1) nutrition for maturing sperm, (2) nutrition for allosperm storage, (3) "nuptial present" to induce sperm recipient to utilize that particular spetm for fertilization. The penis is usually muscular and highly extensible. Often it is equipped with a cuticulat stylet. Size and shape of stylets show great variation (GASCOIGNE, 1974). Penial armature is absent in only two families, Oxynoidae and Hermaeidae; but it is also rare in the Plakobranchidae. In most species the penial opening is located below the base of the right rhinophore.

The female system consists of a small oviduct, a fertilization chamber, an albumen gland, and a mucus gland surrounding the large oviduct. Nothing is known about formation of yolk and albumen. The eggs are fertilized and covered with albumen in the

Table 2. Data on egg diameter and development type in relation to geographical latitude of superfamily Plakobranchoidea.

Taxon	Latitude	Egg diam.	Dev. type
Family Plakobranchidae			
Elysia			
atroviridis	22N	54±6µm	P?
E. australis	35S	64µm	P
E. bangtawaensis	7N	?	P?
E. canguzua	25N	?	P
E. catulus	42N	75.3±3.1µm	P
E. chlorotica	42N	96±8µm	ED
2nd population	42N	79±3µm	P
E. cornigera	25N	105µm	L?/ED?
E. elsiae	20N	ca.80µm	?
E. evelinae	25N	104µm	L/ED
E. expansa	25-35S	?	P
E. gordanae	40N	?	L?
E. hamatanii	30-35N	68µm	P
E. hedgpethi	30N	?	P?
E. japonica	22N	91±4µm	P?
E. leucolegnote	22N	?	?
E. maoria	35S	70µm	P?
E. ornata	25N	?	P
E. papillosa	25N	92µm	L
E. patagonica	46S	?	P?
E. patina	25N	63µm	P
E. serca	25N	61µm	P
E. subornata	25N	120µm	ED
E. thompsoni	25S	62µm	P?
E. timida	40N	120µm	L/ED
E. trisinuata	30-35N	46µm	P
E. tuca	25N	111µm	L
E. viridis	40N	60-70µm	P
Same	50-55N	66µm	P
Same	60N	66-76µm	P
Plakobranchus			
ianthobapsus	20N	?	P?
Thuridilla			
bayeri	10N	80µm	?
T. hopei	40N	200µm	L
T. ratna	10N	80-85µm	?
T. vatae	10N	55-65µm	P
Tridachia			
crispata	25N	205µm	L/ED
Family Boselliidae			
Bosellia leve	28N	64µm	?
B. mimetica	25N	59µm	P
Same	40N	60-75µm	P?
Family Platyhedylidae			
Gascoignella			
aprica	22N	?	P?

Abbreviations as in Table 1.

fertilization chamber. Probably also capsules are secreted here, or in the proximal part of the mucus gland. The eggs do not pass through the albumen gland, which in the non-shelled sacoglossans is highly branched, and usually closely associated with tubules of the digestive gland. Eggs are usually encapsulated singly, though twin embryos occur in some species. During spawning eggs usually pass single-file thtough the oviducal opening, and organisation of eggs within the surrounding mucus may be completed by the mouth atea (some Oxynoacea), or in the spawn groove (some Plakobranchoidea). The chemical and ultrastructural composition of egg masses are unknown. Extracapsular yolk (ECY) is present in one superfamily, Plakobranchoidea. It may form a continuous string or consist of numerous small clumps. It may have the same colout as the eggs or it may have a different colour (Boucher, 1983; Jensen, 1992). Its function and site of production are unknown.

Fertilization is internal, and allosperm may be stored for variable time periods. Animals with no mature oocytes may receive allosperm, thus animals are functionally simultaneous hermaphrodites. Hypodermic impregnation is common, even in species without penial armature. Sperm transfer is usually reciprocal, though not always simultaneously so. Allosperm is stored either in the seminal receptacle or in secondary copulatory butsae formed after the first copulation. These structures are connected to the fertilization chamber. Apparently a mixture of mature, motile sperm and immature, non-motile sperm is delivered during copulation (Jensen, 1986b, 1995). Most sacoglossans also have a large, spherical structure, homologous to the gametolytic sac or bursa copulatrix of other opisthobranchs. In the Sacoglossa this structure is usually called genital receptacle (Gascoigne, 1976) because it contains various "surplus" material (albumen, capsule material, sperm in various stages of degradation). It may have a distal connection to the large oviduct, or a more proximal connection to the fertilization chamber. In a few species both connections exist (Gascoigne, 1979). In a few species the duct of the genital receptacle connects directly to the vaginal opening. The vaginal opening, where present, may also connect to the seminal receptacle, a functional (secondary?) bursa copulatrix (not homologous with genital receptacle), the fertilization chamber, or the pericardium. The actual route taken by allosperm during copulation is unknown. It is also unknown how allospetm injected by hypodermic impregnation finds its way to the sperm storing structure.

Life history data (see Appendix 1 for references):
Data on egg size, development type and geographical latitude are listed in Tables 1-3. In the Oxynoacea (shelled Sacoglossa) and the

Table 3. Data on egg diameter and development type in relation to geographical latitude of superfamily Limapontioidea.

Taxon	Latitude	Egg diam.	Dev. type
Family Polybranchiidae			
Caliphylla			
mediterranea	25N	89µm	P
Same	40N	50-70µm	P?
Cyerce			
antillensis	25N	112µm	L
C. cristallina	40N	60µm	P?
Mourgona			
germaineae	25N	62µm	P
Polybranchia			
pallens	38S	?	ED?
P. viridis	25N	?	P
Family Hermaeidae			
Hermaea bifida	40N	48µm	P?
H. cruciata	25N	77µm	P
Same	37N	100µm	P?
Aplysiopsis			
maculosa	40N	50µm	P?
A. smithi	30N	?	P
A. zebra	25N	71µm	P
Family Limapontiidae			
Alderia			
modesta	42N	70µm	P?
Same	50-55N	78-87µm	P?
Same	56N	62µm	P
Calliopaea			
oophaga	56N	61.7µm	P
Costasiella			
ocellifera	25N	98µm	ED
C. nonatoi	32N	69µm	L
C. pallida	22N	84.6±7.7µm	P?
Ercolania			
boodleae	30-35N	65-100µm	P
E. coerulea	22N	?	P
Same	25N	70µm	P
Same	40N	60µm	P?
E. emarginata	22N	63.4±2.4µm	P
Same	same	58±4µm	P
E. endophytophaga	35S	77±1.4µm	P?
E. felina	40S	56µm	?
E. funerea	25N	59µm	P
Same	40N	75-90µm	P
E. fuscata	25N	60µm	P
Same	42N	64.5±2µm	P?
E. gopalai	10-20N	70µm	P
E. nigra	56N	70µm	P
E. nigrovittata	10-20N	70µm	P
E. translucens	35S	?	P?
Ercolania n.sp.	35S	58.5±2.6µm	P?
Limapontia			
capitata	50-55N	82µm	P
L. depressa	50-55N	80µm	P
L. senestra	50-55N	200µm	AD
Olea			
hansineensis	50N	?	P?
Placida			
cremoniana	40N	50-60µm	P?
P. daguilarensis	22N	56µm	P
P. dendritica	42N	72±5.1µm	P?
Same	50-55N	47-67µm	P
Same	35N	?	P?
P. kingstoni	25N	60µm	P
P. viridis	40N	40-60µm	P?
Stiliger			
aureomarginatus	35S	56±1.6µm	P?
S. berghi	30-35N	65µm	P
S. fuscovittatus	25N	66.5µm	P?
S. llerai	28N	122µm	?
S. verticillata	28N	130µm	?

Abbreviations: AD, ametamorphic direct; others as in Table 1.

Plakobranchoidea (parapodia-bearing Sacoglossa) about 30-40% of the species have non-planktotrophic development. In the Limapontioidea (cerata-bearing Sacoglossa) only 13% of the species have non-planktotrophic development (Table 4). Except for the Hermaeidae, non-planktotrophic development occurs in all families.

In the tropical zone, here broadly designated as 25N-25S, one third of the species have non-planktotrophic development (Table 5). North of 25N 20% of the species have non-planktotrophic development, and south of 25S only 15% of the species have non-planktotrophic development. The tropical zone has the highest number of species, but also the largest fraction (32.5%) of non-planktotrophic development.

In Table 6 species and development type are listed for different zoogeographical regions. Very few species from other regions have known development type. With the exception of Hong Kong, all regions have species with non-planktotrophic development. The Caribbean region apparently has a much larger proportion of non-planktotrophic species.

Egg and capsule size distributions are shown in Fig. 2. Egg size has a skewed, but unimodal distribution, whereas capsule size seems to have a bimodal distribution, corresponding to feeding and non-feeding larvae. In Table 7 egg size and capsule size are correlated with development type. Egg diameter ranges between 40 and

Table 4. Correlation between development type and taxonomic group in the Sacoglossa.

Taxon	Planktotrophic	Non-planktotrophic
Oxynoacea	12 species	7 (8) species
	6 genera	4 genera
Plakobranchoidea	22 species	9 (10) species
	6 genera	3 genera
Limapontioidea	33 species	5 species
	14 genera	4 genera

Table 5. Correlation between development type and latitude in the Sacoglossa (number of species).

Latitude	Planktotrophic	Non-planktotrophic	Total
25N-25S	28	13	41
>25N	24	6	30
>25S	11	2	13
Total	62	21	83

100µm in species with planktotrophic development (mean±s.d. = 59.5±23µm; N=58), and capsule diameters range between 75 and 300µm (mean±s.d. for short diameter = 112.3±30.7µm, and for long diameter =134.8±36.5µm; N=60). In species with lecithotrophic development egg diameter ranges between 69 and 250µm (mean±s.d. = 122.7±51.4µm; N=12), and capsule diameters range between 107 and 422µm (mean±s.d. for short diameter = 254.7±58.3µm, and for long diameter 313.4±72.6µm; N=12). For species with encapsulated direct development egg diameters range between 60 and 205µm (mean±s.d. = 125.4±51.1µm; N=8), and capsule diameters range between 190 and 456µm (mean±s.d. for short diameters = 288±70.5µm, and for long diameter 329.9±60.4µm; N=7). Only one species of Sacoglossa, *Limapontia senestra*, has ametamorphic direct development (CHIA, 1971). This clearly shows that variability is great for all parameters, and there is great overlap in egg and capsule sizes for all development types. In fact, there is very little difference between egg and capsule sizes of the two non-planktotrophic development types. Relative capsule size seems to be a reliable indicator for distinguishing between feeding and non-feeding larval development. Out of 41 planktotrophic species, 34 have ratios of egg / short capsule diameter greater than 0.5, and 14 of 19 non-planktotrophic species have ratios much smaller than 0.5.

Data on duration of embryonic period is given in Table 8. Temperatures have in most cases been "room temperature" of the laboratory in question, which means that it will be higher than natural for temperate species and slightly lower than natural for tropical species. Range for species with non-planktotrophic development is 11-28 days (mean±s.d. = 19.2±6.3 d), and for species with planktotrophic development 4-16 days (mean±s.d. = 8.1±3.2 d); the means differ significantly.

Fecundity differs with size of the parent animal and possibly also with food assimilation. Most species produce one egg mass per day, and spawning begins a few days after copulation. It is unknown how long allosperm can be stored, and how often copulation has to be repeated. Table 9 summarizes information on fecundity in the Sacoglossa. Whether fertilization is controlled by the sperm recipient, i.e. through sperm selection, or the sperm donor, through sperm competition, is also unknown.

DISCUSSION

Planktotrophy is assumed to be ancestral in the Mollusca (STRATHMANN, 1985). Whether it is also ancestral in the Opisthobranchia remains to be determined. The presence of a veliger stage, whether freeswimming or encapsulated, even in species which are shell-less as adults, indicates that the opisthobranch ancestor was planktotrophic. Evolution of non-feeding larvae is seen as an adaptation to stable supplies of adult food and/or high predatory losses in the planktonic stage (STRATHMANN, *op. cit.*; HADFIELD & MILLER, 1987).

In the Sacoglossa non-feeding larvae occur in all major clades; often different development types are found in species of the same genus, and it is not possible to deduct whether planktotrophy is ancestral. True cases of poecilogony are, however, rare; in most cases a species can change between the two non-feeding types, which should not be called poecilogony (BOUCHET, 1989). The only experimentally corroborated case where planktotrophic and encapsulated development occur in one species is *Elysia chlorotica* (WEST *et al.*, 1984). The case of *Elysia subornata (=E. cauze)* (CLARK *et al.*, 1979) has been shown to be two or three sibling species (JENSEN & CLARK, 1983; CLARK, 1984).

It is generally assumed that the incidence of non-planktotrophic development in marine invertebrates increases with latitude. This is known as Thorson's Rule. However, it has been claimed that

Table 6. Geographic variation in development patterns.

A. Japan, 30-35N

Taxon	Development
Julia japonica	P
Berthelinia limax	L
Elysia hamatanii	P
Elysia trisinuata	P
Ercolania boodleae	P
Stiliger berghi	P

Total number: 6; 1 non-planktotrophic

B. Florida, 25N, and Bermuda, 32N

Taxon	Development
Ascobulla ulla	ED
Volvatella bermudae	P
Berthelinia caribbea	L
Lobiger souverbiei	P
Oxynoe antillarum	P
Oxynoe azuropunctata	L
Bosellia mimetica	P
Elysia canguzua	P
Elysia cornigera	L?/ED?
Elysia evelinae	L/ED
Elysia ornata	P
Elysia papillosa	L
Elysia patina	P
Elysia serca	P
Elysia subornata	ED
Elysia tuca	L
Tridachia crispata	L/ED
Polybranchia viridis	P
Caliphylla mediterranea	P
Cyerce antillensis	L
Mourgona germaineae	P
Hermaea cruciata	P
Aplysiopsis zebra	P
Costasiella ocellifera	ED
Costasiella nonatoi	L
Placida kingstoni	P
Ercolania coerulea	P
Ercolania funerea	P
Ercolania fuscata	P

Total number: 29; 12 non-planktotrophic

C. Mediterranean, 40N

Taxon	Development
Oxynoe olivacea	P
Bosellia mimetica	P?
Elysia gordanae	L?
Elysia timida	L/ED
Elysia viridis	P
Thuridilla hopei	L
Caliphylla mediterranea	P?
Cyerce cristallina	P?
Hermaea bifida	P?
Aplysiopsis maculosa	P?
Ercolania coerulea	P?
Ercolania funerea	P
Placida cremoniana	P?
Placida viridis	P?

Total number: 14; 2(3) non-planktotrophic

D. Hong Kong, 22N

Taxon	Development
Lobiger sagamiensis	P?
Elysia atroviridis	P?
Elysia japonica	P?
Elysia leucolegnote	?
Gascoignella aprica	P?
Ercolania coerulea	P
Ercolania emarginata	P
Placida daguilarensis	P
Costasiella pallida	P?

Total number: 9; none non-planktotrophic

E. Western Australia, 25-35S

Taxon	Development
Ascobulla fischeri	P
Volvatella australis	L?
Volvatella ventricosa	P?
Berthelinia darwini	L?
Berthelinia rottnesti	L?
Oxynoe viridis	P?
Elysia australis	P
Elysia expansa	P?
Elysia thompsoni	P?
Stiliger aureomarginatus	P?
Ercolania endophytophaga	P?
Ercolania translucens	P?
Ercolania n.sp.	P?

Total number: 13; 3 non-planktotrophic

this rule does not apply to the Sacoglossa (CLARK & GOETZFRIED, 1978). This has been confirmed by the present study. Though few species have been studied from the southern hemisphere, the fraction of species with non-planktotrophic development is distinctly higher in the tropical zone than in temperate zones (Table 5). Unfortunately no sacoglossan species has an exclusively polar distribution.

The high incidence of non-planktotrophy in the Caribbean (Table 6B) can be interpreted as an adaptation to temporally stable, but spatially restricted adult food sources, i.e. offspring should be retained in the area of the parents (CLARK & GOETZFRIED, 1978), and sufficient nutritional material can be allocated to developing embryos to suppress the feeding planktonic stage. In fact, the number of green algal species of suitable morphology (see JENSEN, 1997b) is very high in the Caribbean, but also in Western Australia (WOMERSLEY, 1984). Whether the high incidence of non-planktotrophic development in the Caribbean is due to local, sympatric speciation can be clarified by application of cladistic analysis. One working hypothesis would be that each of the non-planktotrophic species of e.g. *Elysia* have planktotrophic sister-species in neighbouring areas; an alternative hypothesis, also supporting local speciation, would be that the non-planktotrophic species are more closely related to one another than to any congener from other regions. Unfortunately the anatomy of the Caribbean species of *Elysia* has not been described in detail, and a preliminary cladistic analysis based on literature information, and including several Indo-West Pacific species of *Elysia* did not give meaningful results.

It has been claimed previously that relative capsule volume is a better indicator of development type in the Sacoglossa than egg diameter (CLARK & JENSEN, 1981). The present study has confirmed this. Although average egg diameter is significantly smaller in planktotrophic species than in non-planktotrophic species, ranges overlap considerably (Table 7). Only 7 planktotrophic species have short capsule diameters greater than twice the egg diameter. One of these species is *Elysia chlorotica* in which populations with different development types have been described (WEST *et al.*, 1984). This indicates that speciation may be in progress. Capsule size may be a plastic character which can adapt locally to food availability, and increasing capsule size to include more nutritional material (albumen) may reduce the need for a post-hatching feeding veliger. Three of the 7 planktotrophic species with large capsules are congeners of the apparently cosmopolitan *Placida dendritica*, and they may be recent speciations, one in the Caribbean, *P. kingstoni*, one in the Mediterranean, *P. viridis*, and one in the South China Sea, *P. daguilarensis*. Again application of cladistic analysis may clarify whether widely separated populations of *P. dendritica* gave rise to the other 3 species. Two of the 7 species belong to the genus *Hermaea*, and non-planktotrophic development does not occur in the family Hermaeidae. In this connection it should be noticed that the albumen gland in this family is less branched than in other familes, and does not enter the cerata (JENSEN, 1997b). Thus absence of non-planktotrophic larvae may be due to inability to produce sufficient nutritional material.

As the albumen gland in most sacoglossans branches extensively in close association with the digestive gland, it may be speculated

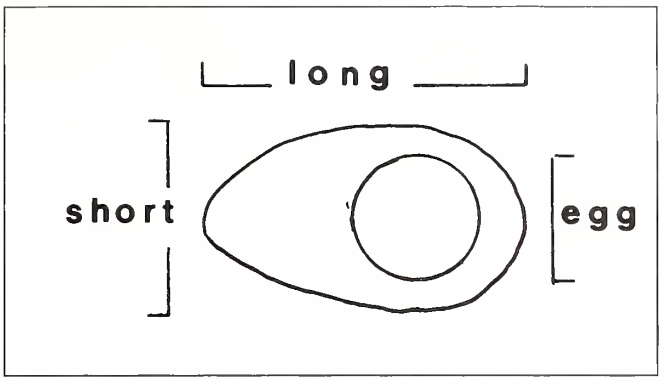

Fig. 1. Measurements used on sacoglossan eggs and egg capsules.

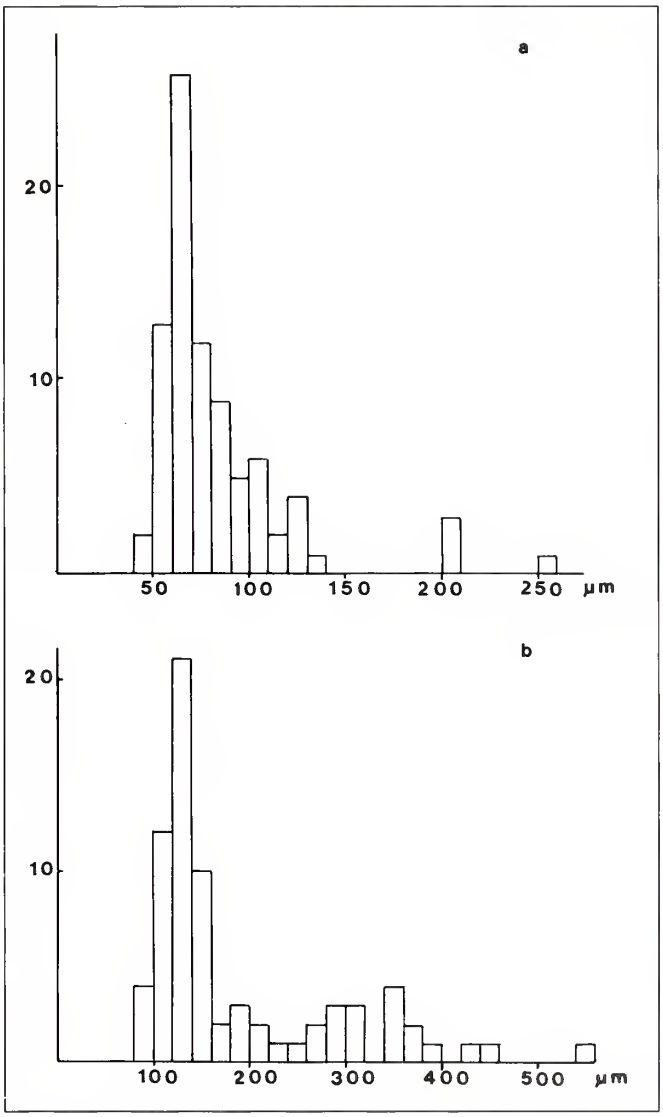

Fig. 2. Size-frequency distribution of (a) egg diameters and (b) capsule diameters in the Sacoglossa. Long diameters have been used where available. Data used is listed in Table 7.

that production of albumen is correlated with food intake and/or production by functional kleptoplastids. Plasticity of the size of egg capsules would be a prerequisite for allocating larger amounts

Table 7. Correlation of egg diameter, capsule size and development type in the Sacoglossa

Taxon	Egg diameter	Capsule size	Dev. type
Volvatellidae			
Ascobulla			
fischeri	?	200µm	P
A. ulla	60 & 84µm	190x250µm	ED
Volvatella			
australis	100.8±6.2µm	236x272µm	L?
V. bermudae	66µm	98x106µm	P
V. ventricosa	97.2±10.5µm	150x204µm	P?
Juliidae			
Julia japonica	65µm	100x150µm	P
Berthelinia			
australis	54µm	?	P?
B. caribbea	100µm	250x310µm	L
B. darwini	102.8±5.9µm	240x346µm	L?
B. ganapati	50µm	90µm	P
B. limax	250µm	270x380µm	L
B. rottnesti	?	203x274µm	L?
Oxynoidae			
Oxynoe			
antillarum	63µm	97x114µm	P
O. azuropunctata	120 & 113µm	280x370µm	L
O. olivacea	62-69µm	91-109x121-125µm	P
Same	250µm	500µm	?
O. viridis	56-72µm	100x147 & 113x137µm	P
Lobiger			
sagamiensis	?	108x142µm	P?
L. souverbiei	56µm	88x99µm	P
Plakobranchidae			
Elysia			
atroviridis	54±6µm	143x173µm	P?
E. australis	64µm	88x104µm	P
E. bangtawaensis	?	127x106µm	P
E. catulus	75.3±3.1µm	?	P
E. chlorotica	96±8µm	309±8 & 349±24µm	ED
2nd population	79±3µm	164±12 & 192±36µm	P
E. cornigera	105µm	268x291µm	L?/ED?
E. evelinae	104µm	273x294µm	L/ED
E. expansa	?	129x144µm	P
E. hamatanii	68µm	115-140µm	P
E. hedgpethi	?	95x120µm	P?
E. japonica	91±4µm	166x196µm	P?
E. maoria	70µm	?	P?
E. papillosa	92µm	242x286µm	L
E. patagonica	?	250-300µm	P?
E. patina	63µm	0.00072mm^3	P
E. serca	61µm	109x133µm	P
E. subornata	120µm	400x456µm	ED
E. thompsoni	62µm	115x132µm	P?
E. timida	120µm	200x300µm	ED
Same	70µm	100-125µm	L
E. trisinuata	46µm	77-85µm	P?
E. tuca	111µm	319x361µm	L?
E. viridis	60-76µm	100x180µm	P
Thuridilla			
bayeri	80µm	120-140µm	?
T. hopei	200µm	?	L
Tridachia			
crispata	205µm	276x341µm	L/ED

Table 7. Correlation of egg diameter, capsule size and development type in the Sacoglossa

Taxon	Egg diameter	Capsule size	Dev. type
Boselliidae			
Bosellia			
mimetica	59-75µm	75-97x90-114µm	P
Platyhedylidae			
Gascoignella			
aprica	?	88x103µm	P?
Polybranchiidae			
Caliphylla			
mediterranea	89µm	117x142µm	P?
Same	50-70µm	70x100 & 110x120µm	P?
Cyerce			
antillensis	112µm	334x422µm	L
Mourgona			
germaineae	62µm	104x130µm	P
Hermaeidae			
Hermaea bifida	48µm	104x128µm	P?
H. cruciata	77µm	165x230µm	P?
Aplysiopsis			
maculosa	50µm	?	P?
A. smithi	?	85x125µm	P
A. zebra	71µm	92x138µm	P
Limapontiidae			
Alderia			
modesta	62-87µm	?	P
Calliopaea			
oophaga	61.7µm	96x85µm	P
Costasiella			
ocellifera	98µm	307x340µm	ED
C. nonatoi	69µm	107x127µm	L
C. pallida	84.6±7.7µm	107x133 & 103.1x128.4µm	P?
Ercolania			
boodleae	65-100µm	100-150µm	P?
E. coerulea	60-70µm	80-123x110-137µm	P
E. emarginata	58-65µm	104-122x124-142µm	P?
E. endophytophaga	77±1.4µm	109-133x128-148µm	P?
E. funerea	59-90µm	90-110x110-146µm	P
E. fuscata	60-65µm	85x115µm	P
E. gopalai	70µm	175µm	P?
E. nigra	70µm	100µm	P
E. nigrovittata	70µm	120x145µm	P?
E. translucens	?	110x123µm	P?
Ercolania n.sp.	58.5±2.6µm	89x114µm	P?
Limapontia			
capitata	82µm	100µm	P
L. depressa	80µm	120µm	P
L. senestra	200µm	350x550µm	AD
Placida			
cremoniana	50-60µm	110x140µm	P?
P. daguilarensis	56µm	117x136µm	P
P. dendritica	47-77µm	90x105µm	P?
P. kingstoni	60µm	123x125µm	P
P. viridis	40-60µm	130x140µm	P?
Stiliger			
aureomarginatus	56±1.6µm	96x122 & 99x127µm	P?
S. berghi	65µm	100-130µm	P?
S. fuscovittatus	66.5µm	?	P?

Table 8. Development times related to development type in the Sacoglossa.

Taxon	Developm. time	Temp.	Developm. type
Oxynoacea			
Ascobulla			
fischeri	8-9d	25C	P?
Volvatella			
ventricosa	17d	?	P
Julia japonica	10-11d	?	P
Berthelinia			
australis	13d	21C	P?
Oxynoe			
azuropunctata	28d	18-21C	L/ED
O. olivacea	7-8d	22C	P
O. panamensis	13d	21C	P
O. viridis	6-7d	22-23C	P
Plakobranchoidea			
Bosellia			
mimetica	13d	16C	P?
Plakobranchus			
ianthobapsus	8d	?	P?
Thuridilla hopei	20d	21C	L
T. vatae	5d	?	P
Elysia australis	6-7d	22-23C	P
E. bangtawaensis	7-8d	20-27C	P
E. chlorotica	14d	?	ED
same, 2nd pop.	7-8d	?	P
E. elsiae	5d	?	P
E. evelinae	11-14d	18-21C	L/ED
E. hamatanii	6d	15-25C	P
E. hedgpethi	14d	?	P?
E. maoria	6d	22-23C	P
E. timida	16-21d	?	L/ED
E. trisinuata	4d	23-27.5C	P
E. viridis	6d	16C	P
same	15-16d	10-12C	P
Limapontioidea			
Cyerce			
cristallina	22d	16C	?
Caliphylla			
mediterranea	9-14d	16C	P?
Hermaea bifida	10d	?	P?
H. cruciata	5d	19.5C	P
Aplysiopsis			
smithi	5-6d	?	P
Alderia modesta	5-6d	14C	P
Calliopaea			
oophaga	4d	20C	P
Ercolania			
boodleae	7d	17-20C	P
E. coerulea	11-13d	16C	P?
E. emarginata	7d	18C	P
E. felina	7-9d	13.2C	P?
E. gopalai	5d	?	P
E. nigra	5d	19-22.5C	P
E. nigrovittata	4d	25.5-27C	P
Limapontia			
capitata	12d	10-14C	P
same	8d	19-21C	P
L. depressa	10d	10-14C	P
same	7d	19-21C	P
L. senestra	24-25d	10-14C	AD
Olea			
hansineensis	6d	?	P
Placida			
cremoniana	12d	16C	P?
P. dendritica	9d	13-15C	P
P. viridis	8d	16C	P?
Stiliger berghi	9d	10-20C	P

Table 9. Fecundity expressed as number of eggs in one egg mass related to adult size.

Taxon	No. eggs/mass	Adult size
Oxynoacea		
Ascobulla ulla	84-1900	?
Volvatella australis	210-420	12 mm
V. ventricosa	570-1060	ca. 10 mm
Berthelinia australis	50	1 mm
B. caribbea	14-80	?
B. darwini	45-96	4-8 mm
B. ganapati	500-3520	3.7-7 mm
B. limax	11-470	2.7-7.2 mm
Julia japonica	<100->2000	?
Oxynoe antillarum	1940	ca. 20 mm
O. azuropunctata	53-2755	10-40 mm
O. olivacea	1000-5000	20-40 mm
O. viridis	640-1500	20-40 mm
same	30.600	?
Lobiger souverbii	1630	?
L. sagamiensis	6000	?
Plakobranchoidea		
Gascoignella aprica	600	5-8 mm
Elysia australis	420-3000	ca. 10 mm
E. chlorotica	176±113	7.6±2.6 mm
same, 2nd population	8902±7258	20±8 mm
E. cornigera	77-137	?
E. leucolegnote	1070	ca. 30 mm
E. maoria	1000-6000	?
E. patina	6230	?
E. subornata	52-1065	?
E. timida	70-230	25 mm
E. tuca	290	?
Thuridilla bayeri	2500	16 mm
T. ratna	2250	14-15 mm
Tridachia crispata	1020	?
Limapontioidea		
Mourgona germaineae	1960	10-20 mm
Polybranchia pallens	12-35	?
Hermaea cruciata	340	?
Costasiella mandorahae	70	4-5 mm
Costasiella ocellifera	88	?
C. pallida	500	?
Aplysiopsis zebra	5740	?
Placida daguilarensis	63-540	5-20 mm
P. kingstoni	1590	?
Stiliger fuscovittatus	70	?
Calliopaea oophaga	31-1458	3-8 mm
Olea hansineensis	250-600	4-9 mm
Ercolania boodleae	35-7700	4-20 mm
E. coerulea HK	1100	?
same, Fla.	1570	?
E. emarginata	1350	7-15 mm
E. endophytophaga	77-117	3-5 mm
E. funerea	800	?
E. fuscata	70	?
E. gopalai	700-1500	11-12 mm
E. nigra	3435	7-13 mm
Limapontia capitata	31-720	?
same	10-450	?
L. depressa	73-950	?
same	49-199	?
Limapontia senestra	3-26(40)	?

of albumen to individual embryos. Alternatively a higher number of eggs could be produced.

Extracapsular yolk (ECY) is produced in many species of the Plakobranchoidea. It has been speculated that this supplies additional nutrition for embryos or hatching larvae/ juveniles (Clark *et al.*, 1979; Marin & Ros, 1993). However, ECY is found in many species with planktotrophic development (Boucher, 1983; Jensen, 1997a). An extended benthic embryonic phase would seem to require parental investment in protection from predators, and it may be suggested that the function of ECY is defensive, either containing toxins produced by parent animal or providing food for predatory ciliates or bacteria. Unfortunately it is not known which structure in the reproductive system produces this ECY, and hence it is unknown whether the amount produced can be changed with changes in food availability. Its distribution in just one superfamily indicates a monophyletic origin, but arrangement and colouration differ among species.

Protoconchs have been used extensively in the prosobranchs to indicate development type (Jablonski & Lutz, 1983). In opisthobranchs protoconchs usually have few whorls and no ornamentation. In the Sacoglossa protoconchs always have less than two whorls (Jensen, 1997b), and thus they cannot be used to indicate development type. Other criteria that have been used to indicate non-planktotrophic development type include appearance of eyes prior to hatching, and development of a propodium enabling pedal crawling (Thompson, 1967). Also, a reduced velum size indicates non-feeding.

A comprehensive review of reproduction in the Sacoglossa must encompass morphology of reproductive systems and reproductive behaviour as well as life history traits. The morphological characters showing the greatest interspecific variability are penial armature and arrangement of allosperm receptacles. Penial armature occurs in all major sacoglossan clades; it is absent in the Hermaeidae and Oxynoidae (Jensen, 1997b). Loss of penial armature may be an important process in speciation as it may be a simple mutation and most likely ensures reproductive isolation. Size and shape

APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
Suborder Oxynoacea		
	Family Volvatellidae	
Ascobulla fischeri (Adams & Angas, 1864)	W Australia	Jensen & Wells 1990
Ascobulla ulla (Marcus & Marcus, 1970)	Florida	Clark & Jensen 1981; DeFreese & Clark 1991
Volvatella australis Jensen, 1997	W Australia	Jensen 1997a
Volvatella bermudae Clark, 1982	Bermuda	Clark & Jensen 1981
Volvatella ventricosa Jensen & Wells, 1990	W Australia	Jensen 1997a
	Family Juliidae	
Julia japonica Kuroda & Habe, 1951	Japan	Kawaguti & Yamasu 1966
Berthelinia australis (Burn, 1960)	SE Australia	Wisely 1962
Berthelinia caribbea Edmunds, 1963	Florida	Clark & Jensen 1981
Berthelinia darwini Jensen, 1997	W Australia	Jensen 1997a
Berthelinia ganapati Sarma, 1975	India	Sarma 1975
Berthelinia limax (Kawaguti & Baba, 1959)	Japan	Kawaguti & Yamasu 1960
Berthelinia rottnesti Jensen, 1993	W Australia	Jensen 1993
	Family Oxynoidae	
Oxynoe antillarum Mörch, 1863	Florida	Clark & Jensen 1981; DeFreese & Clark 1991
Oxynoe azuropunctata Jensen, 1980	Florida	Clark & Jensen 1981
Oxynoe olivacea Rafinesque, 1819	Mediterranean	present study
Same	Canary Island	Marin & Ros 1988
Oxynoe panamensis Pilsbry & Olsson, 1943	Gulf of California	Jensen 1980
Oxynoe viridis (Pease, 1861)	W Australia	Jensen 1997a
Same	E Australia	Rose 1985
Same		
Lobiger sagamiensis Baba, 1952	Hong Kong	Jensen 1985
Lobiger souverbiei Fischer, 1856	Florida	Clark & Jensen 1981; DeFreese & Clark 1983

APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
Suborder Plakobranchacea		
Superfamily Plakobranchoidea		
	Family Plakobranchidae	
Elysia atroviridis Baba, 1955	Hong Kong	Jensen 1985
Elysia australis (Quoy & Gaimard, 1832)	W Australia	Jensen 1997a
Same	E Australia	Rose 1985
Same		
Elysia bangtawaensis Swennen, 1997	Thailand	Swennen 1997
Elysia canguzua Marcus, 1955	Florida	Jensen & Clark 1983
Elysia catulus (Gould, 1870)	Conn. USA	Clark 1975
Elysia chlorotica Gould, 1870	Mass. USA	West *et al.* 1984
Elysia cornigera Nuttall, 1989	Florida	Nuttall 1989
Elysia elsiae Ostergaard, 1955	Hawaii	Ostergaard 1950
Elysia evelinae Marcus, 1957	Florida	Clark & Jensen 1981
Elysia expansa (O'Donoghue, 1924)	W Australia	present study
Elysia gordanae Thompson & Jaklin, 1988	Mediterranean	Marin & Ros 1988
Elysia hamatanii Baba, 1957	Japan	Hamatani 1960
Elysia hedgpethi Marcus, 1961	S California	Greene 1968
Elysia japonica Eliot, 1913	Hong Kong	Jensen 1985
Elysia leucolegnote Jensen, 1990	Hong Kong	Jensen 1990
Elysia maoria Powell, 1937	E Australia	Rose 1985
Elysia ornata (Swainson, 1840)	Florida	Jensen & Clark 1983
Elysia papillosa Verrill, 1901	Florida	Clark & Jensen 1981
Elysia patagonica Munian & Ortea, 1997	Argentina	Munian & Ortea 1997
Elysia patina Marcus, 1980	Florida	DeFreese & Clark 1983
Elysia serca Marcus, 1955	Florida	Clark & Jensen 1981
Elysia subornata Verrill, 1901	Florida	Clark & Jensen 1981; DeFreese & Clark 1991
Elysia thompsoni Jensen, 1993	W Australia	Jensen 1993

APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
Elysia timida Risso, 1818	Mediterranean	Clark & Jensen 1981; Marin & Ros 1993
Elysia trisinuata Baba, 1949	Japan	Hamatani 1967
Elysia tuca Marcus & Marcus, 1967	Florida	Clark & Jensen 1981; DeFreese & Clark 1983
Elysia viridis Montagu, 1804	Mediterranean	Schmekel & Portmann 1982
Same Same	UK	Kress 1972
Same Same	Norway	Hagerman 1970
Plakobranchus ianthobapsus Gould, 1852	Hawaii	Ostergaard 1950
Thuridilla bayeri (Marcus, 1965)	Marshall Island	Johnson & Boucher 1983
Thuridilla hopei (Verany, 1853)	Mediterranean	Thompson & Salghetti-Drioli 1984
Thuridilla ratna (Marcus, 1965)	Marshall Islands	Johnson & Boucher 1983
Thuridilla vatae (Risbec, 1928)	Marshall Islands	Johnson & Boucher 1983
Tridachia crispata Mörch, 1863	Florida	Clark & Jensen 1981; DeFreese & Clark 1983
	Family Bosellidae	
Bosellia leve Fernandez-Ovies & Ortea, 1986	Canary Island	Fernandez-Ovies &Ortea 1986
Bosellia mimetica Trinchese, 1891	Florida	Clark & Jensen 1981
Same Same	Mediterranean	Schmekel & Portmann 1982
	Family Platyhedylidae	
Gascoignella aprica Jensen, 1985	Hong Kong	Jensen 1985
Superfamily Limapontioidea		
	Family Polybranchiidae	
Caliphylla mediterranea Costa, 1867	Florida	Clark & Jensen 1981
Same Same	Mediterranean	Schmekel & Portmann 1982
Cyerce antillensis Engel, 1927	Florida	Clark & Jensen 1981
Cyerce cristallina (Trinchese, 1881)	Mediterranean	Schmekel & Portmann 1982
Mourgona germaineae Marcus & Marcus, 1970	Florida	Clark & Jensen 1981
Polybranchia pallens (Burn, 1957)	SE Australia	Burn 1998
Polybranchia viridis (Deshayes, 1857)	Florida	Clark 1994

APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
	Family Hermaeidae	
Hermaea bifida (Montagu, 1815)	Mediterranean	Schmekel & Portmann 1982
Hermaea cruciata Gould, 1870	Florida	Clark & Jensen 1981
Same Same	Chesapeake (USA)	Vogel 1971
Hermaea evelinemarcusae Jensen, 1993	W Australia	Jensen 1993
Aplysiopsis maculosa (Trinchese, 1874)	Mediteranean	Kress 1972
Aplysiopsis smithi (Marcus, 1961)	S California	Greene 1968
Aplysiopsis zebra Clark, 1982	Florida	Clark & Jensen 1981
	Family Limapontiidae	
Alderia modesta (Lovén, 1844)	Connecticut (USA)	Clark & Goetzfried 1978
Same Same	UK	Kress 1972
Same *Same*	Denmark	Rasmussen 1951
Calliopaea oophaga Lemche, 1974	Denmark	Jensen 1986a
Costasiella ocellifera (Simroth, 1895)	Florida	Clark & Jensen 1981; DeFreese & Clark 1983
Costasiella mandorahae Jensen, 1997	N Australia	Jensen 1997c
Costasiella nonatoi Marcus & Marcus, 1960	Bermuda	Clark & Jensen 1981
Costasiella pallida Jensen, 1985	Hong Kong	Jensen 1990; present study
Ercolania boodleae (Baba, 1938)	Japan	Hamatani 1960; Usuki 1977
Ercolania coerulea Trinchese, 1893	Hong Kong	Jensen 1985
Same Same	Florida	Clark & Jensen 1981
Same Same	Mediterranean	Schmekel & Portmann 1982
Ercolania emarginata Jensen, 1985	Hong Kong	Jensen 1985; present study
Ercolania endophytophaga Jensen, 1999	W Australia	present study
Ercolania felina (Hutton, 1882)	New Zealand	Trowbridge 1995
Ercolania funerea (Costa, 1867)	Florida	DeFreese & Clark 1983
Same Same	Mediterranean	Schmekel & Portmann 1982
Ercolania fuscata (Gould, 1870)	Florida	Clark & Jensen 1981
Same Same	Conn. USA	Clark 1975

APPENDIX 1 - Sources of data used in present study

Taxon	Location	References
Ercolania gopalai Rao, 1937	India	Rao 1937
Ercolania nigra Lemche, 1935	Denmark	Rasmussen 1951
Ercolania nigrovittata Rao & Rao, 1963	India	Rao & Rao 1963
Ercolania translucens Jensen, 1993	W Australia	present study
Ercolania n.sp.	W Australia	present study
Limapontia capitata (Müller, 1774)	UK	Chia 1971
Limapontia depressa Alder & Hancock, 1862	UK	Chia 1971
Limapontia senestra (Quatrefages, 1844)	UK	Chia 1971
Olea hansineensis Agersborg, 1823	Vancouver	Chia & Skeel 1973; Crane 1971
Placida cremoniana (Trinchese, 1893)	Mediterranean	Schmekel & Portmann 1982
Placida daguilarensis Jensen, 1990	Hong Kong	Jensen 1990
Placida dendritica (Alder & Hancock, 1843)	Connecticut USA	Clark 1975
Same Same	UK	Kress 1971
Same Same	California	Greene 1968
Placida kingstoni Thompson, 1977	Florida	Clark & Jensen 1981
Placida viridis Trinchese, 1873	Mediterranean	Schmekel & Portmann 1982
Stiliger aureomarginatus Jensen, 1993	W Australia	Jensen 1993; present study
Stiliger berghi Baba, 1937	Japan	Hamatani 1963
Stiliger fuscovittatus Lance, 1962	Florida	Clark & Goetzfried 1978
Stiliger llerai Ortea, 1981	Canary Islands	Ortea 1981
Stiliger verticillata (Ortea, 1981)	Canary Islands	Marin & Ros 1988

of penial armature is very important in species identification, and probably also serves in recognition of conspecifics. It should be noted that hypodermic impregnation may occur in sacoglossans without penial armature (JENSEN, 1986b). Whether this involves enzymatic action from one or both copulatory partners is unknown. The highly variable arrangement of allosperm receptacles may also serve to ensure reproductive isolation. However, it may also allow the sperm recipient to select among sperm received from different partners. It is unknown whether single egg masses may be fertilized by sperm from more than one sperm donor.

Copulatory behaviour has recently been reviewed (JENSEN, 1999). Most species have a precopulatory mate identification behaviour. The most common copulatory position is with animals facing in opposite directions and right sides touching. Intromission may be unilateral or reciprocal. In the Limapontioidea copulation is usually brief, less than 30 seconds to a few minutes; in the Plakobran-

choidea and Oxynoacea copulation may last more than one hour. Sperm transfer is usually reciprocal, though not always simultaneously so. Allosperm can be stored for variable lengths of time, but no formal studies exist on this aspect. Also, nothing is known about factors controlling fertilization, i.e. whether sperm from different copulations compete, or whether the sperm recipient selects sperm from a particular copulation. These are important aspects for understanding evolution, and it will be worthwhile to study this in the future.

Reproductive effort, that is the total amount of energy allocated to reproduction, has been examined in Caribbean sacoglossans (DEFREESE & CLARK, 1983). It seems to depend more on the size of the parent than on development type.

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Some comparative histological aspects of the dendrodorid genera *Doriopsilla and Dendrodoris* (Opisthobranchia: Nudibranchia)

Gilianne D. Brodie

KEY WORDS: Histology, *Dendrodoris*, *Doriopsilla*, Nudibranchia, dendrodorid, radula-less dorids

ABSTRACT The nudibranch family Dendrodoridae O'Donoghue 1924 consists of two genera, *Dendrodoris* Ehrenberg 1831 and *Doriopsilla* Bergh 1880. These taxa are notable because they lack radula and possess highly modified digestive systems. At least one species of *Dendrodoris* is also novel, in possessing symbiotic bacteria within a vestibular gland of the female reproductive system. The digestive and reproductive systems of several dendrodorids were examined by methacrylate resin histology. This study was underraken to search for new character sets to address the phylogenetic placement of dendrodorids within the radula-less dorids and to make a comparison between features of the two-dendrodorid genera. Methacrylate resin histology is particularly useful for investigation of glandular tissue at a cellular level. The position of glandular tissue is very relevant to the separation of *Doriopsilla* from its sister taxon *Dendrodoris*. Studies of gross morphology have indicated that the placement of glands within the digestive system of *Doriopsilla* is different from that of *Dendrodoris*, however, to date no comparison of these organ systems by histological means has been undertaken. The study found that in *Doriopsilla* the oral glands are an integral part of the oral tube and have a different cell structure to those found in *Dendrodoris* where the oral glands are clearly separated from the oral tube. In addition the extent of glandular and muscle tissue within the pharynx and oesophagus of the two genera is very different, suggesting that the function of the respective components of the anterior digestive system differ between the two genera. The investigation also found that the genera differ in the structural arrangement of their ovotestis, kidney and digestive gland tissue. This study provides basic information related to the function of digestive and reproductive systems in dendrodorid nudibranchs and will improve the phylogenetic resolution of these taxa particularly by indicaring which glandular structures are likely to be homologous. These results also provide information vital to clarifying the phylogenetic relationship of dendrodorids to other radula-less dorids.

RIASSUNTO La famiglia Dendrodoridae O'Donoghue 1924 è costituita dai generi *Dendrodoris* Ehrenberg, 1831 e *Doriopsilla* Bergh, 1880. Questi due taxa presentano caratteristiche anatomiche particolari, mancano di radula e possiedono un sistema digestivo assai modificato. Almeno una specie di *Dendrodoris* inoltre è particolare in quanto presenta, all'interno della ghiandola vestibolare dell'apparato genitale femminile, batteri simbionti. I sistemi riproduttivi e digestivi di diverse specie di dendrodoridi sono stati esaminati dopo fissaggio in resina metacrilica, particolarmente adatta per studiare il tessuto ghiandolare a livello cellulare. Scopo di questo studio, oltre ad un confronto anatomico tra i due generi, è quello di definire nuovi caratteri utili a valutare la posizione filogenetica dei dendrodoridi nell'ambito dei doridacei senza radula. La posizione del tessuto ghiandolare è molto importante nella separazione tra i due generi: studi di morfologia di base indicano che la localizzazione delle ghiandole all'interno del sistema digestivo in *Doriopsilla* è differente rispetto a *Dendrodoris*, ma nessun confronto a livello istologico era mai staro condotto. I risultati di questo studio rivelano come le ghiandole orali in *Doriopsilla* siano parte integrante del tubo orale ed hanno una struttura cellulare differente da quella presente in *Dendrodoris*, dove le ghiandole orali sono nettamente separate dal tubo orale.
Inoltre lo sviluppo dei tessuti ghiandolari e muscolari all'interno della faringe e dell'esofago è diverso nei due generi, suggerendo che questi abbiano una funzione diversa nei sistemi digestivi anteriori dei due generi. La ricerca ha anche evidenziato come i due generi differiscano nell'organizzazione strutturale dell'ovotestis, del rene e della ghiandola digestiva. Questo studio, oltre a fornire indicazioni di base sul funzionamento dei sistemi ghiandolari e riproduttivi nei dendrodoridi, indica, a livello d'analisi filogenetica, quali strutture ghiandolari possano essere considerate omologhe, contribuendo dunque a chiarire i rapporti filogenetici tra i dendrodoridi e gli altri doridacei senza radula.

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INTRODUCTION

The molluscan order Nudibranchia contains approximately 190 described genera (WÄGELE & WILLAN, 2000). Eleven of these genera (*Melibe, Tethys, Phyllidia, Fryeria, Phyllidiella, Phyllidiopsis, Ceratophyllidia, Reticulidia, Dendrodoris, Doriopsilla and Mandelia*) are notable because they have secondarily lost the characteristic molluscan radula. The latter nine genera are dorids, traditionally grouped together by radula absence and an adaptation to suctorial feeding. Controversy exists over this grouping, with results from the recent literature conflicting. VALDÉS (1996) and VALDÉS & GOSLINER (1999) support common ancestry while, BRUNCKHORST (1993) and RUDMAN (1998) oppose it. New phylogenetic character sets, with which to examine the taxa in more detail, are obviously required.

This study continues a search for new character sets by examining several members of the genera *Dendrodoris* and *Doriopsilla* by methacrylate resin histology. An extensive investigation of the Indo-Pacific dendrodorid *Dendrodoris nigra* (Stimpson), using this histological technique, revealed features contrary to those found in other cryptobranch dorids (WÄGELE *et al.*, 1999). These features include: the composition of the notal epithelium; the absence of "special" vacuolated cells; the cell structure of the salivary glands; the density of gland cells in the oesophagus; the muscle layers of the oesophagus; the size and structure of gill retractor muscles; the appearance of the oral glands; and the intermingled position of the gonad, digestive gland and kidney tissue.

In this current paper, data from the histological examination of the anterior digestive system and two features of the reproductive system (distal oviduct and gonad position) are presented for several species of dendrodorid i.e., *Dendrodoris fumata* (RÜPPELL & LEUCKART, 1828) (grey and orange/red form), *Dendrodoris albobrunnea* ALLAN, 1933, *Dendrodoris guttata* (ODHER, 1917), *Doriopsilla miniata* (ALDER & HANCOCK, 1864) and *Doriopsilla gemela* GOSLINER, SCHAEFER & MILLEN, 1999. This data reveals both considerable similarities and differences between the two-dendrodorid genera.

MATERIAL AND METHODS

Two specimens of *Doriopsilla miniata* (length of living specimens 25, 26 mm) from Hastings Point, New South Wales, Australia, collected in July 1991 and January 1998; one specimen of *Doriopsilla gemela* (length of preserved specimen 23 mm) from Bahia de Los Angeles, Baja California, Mexico collected in June 1996; one specimen of *Dendrodoris albobrunnea* (length of living specimen 49 mm) from Pioneer Bay, Orpheus Island, Palm Group, Great Barrier Reef, Australia, collected September 15 1993; 2 specimens of *Dendrodoris guttata* (both specimens 41 mm length alive) from Julian Rocks near Cape Byron, New South Wales, Australia, collected 30 January 1983; 1 specimen of *Dendrodoris fumata* [orange/red form] (length of living specimen 27 mm) from Bay Rock, off Magnetic Island, Great Barrier Reef, Australia, collected 14 August 1994; 1 specimen *Dendrodoris fumata* [grey form] (length of living specimen 37 mm) from Horseshoe Bay, Magnetic Island, Great Barrier Reef, Australia, collected 2 August 1997. All specimens, except *Doriopsilla gemela*, were preserved in formalin seawater for a minimum of 4 weeks; the specimen of *D. gemela* was preserved in Bouin's fixative before transfer to alcohol. All specimens were progressively dehydrated over a 9-hour period utilizing steadily increasing concentrations of ethanol. Whole dehydrated animals were embedded in hydroxyethylmethacrylate (Kulzer) before

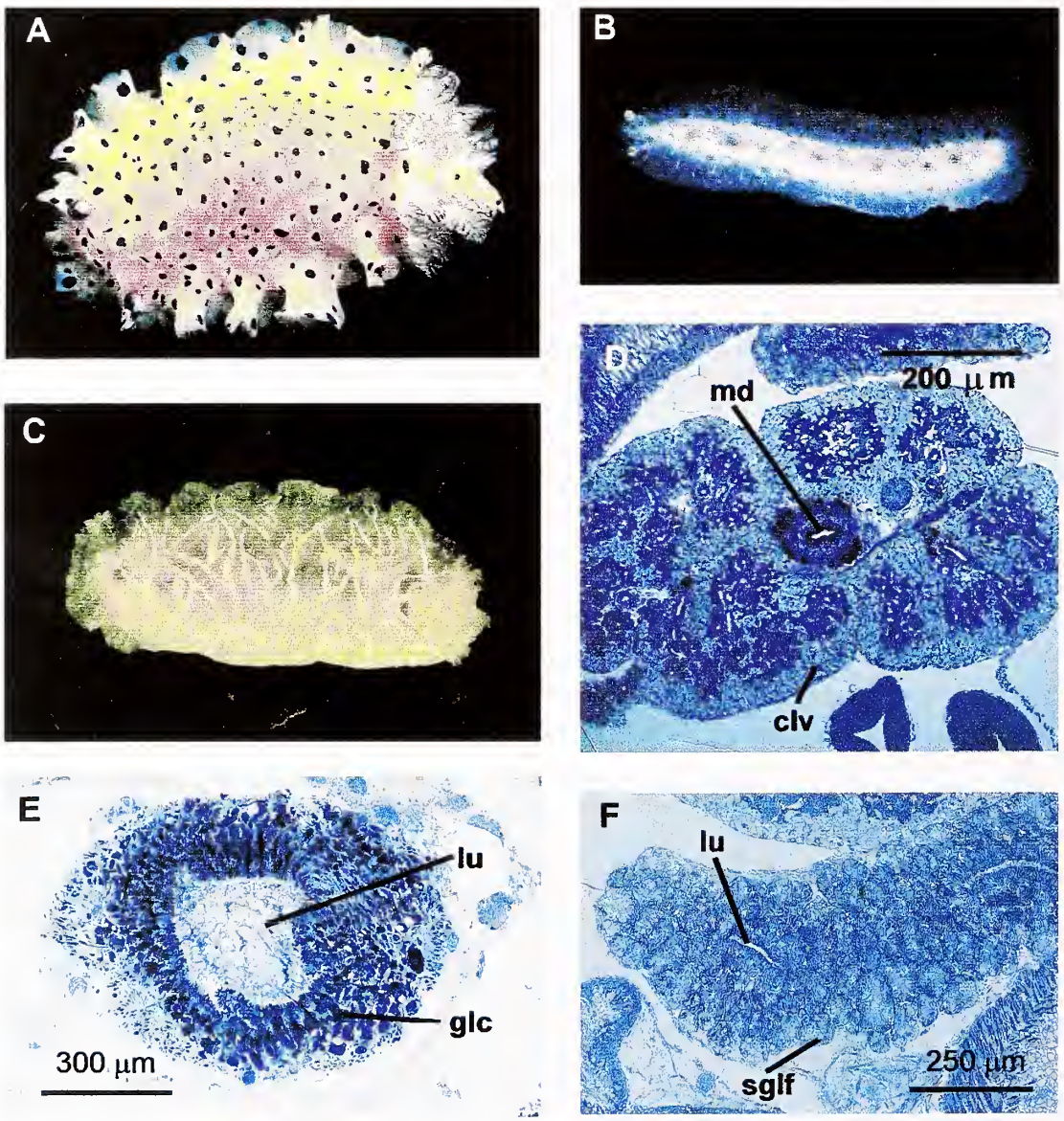

Figure 1. A. Photograph showing the external appearance of a living *Dendrodoris guttata* (length 41 mm) B. Photograph showing the external appearance of a living *Dendrodoris albobrunnea* (length 30 mm) C. Photograph showing the external appearance of a living *Doriopsilla miniata* (length 25mm) D. *A histological cross-section of the oral (ptyaline) glands in Dendrodoris albobrunnea* E. *A histological cross-section of the oral tube and associated oral glands in Doriopsilla miniata* F. A histological section of the salivary glands of *Dendrodoris fumata* (red form). Abbreviations: clv = cells with large vacuoles, glc = gland cell, lu = lumen, md = muscular duct, sglf = salivary gland follicle.

Table 1. A comparative summary of the results of a histological investigation of the anterior digestive system, and parts of the reproductive system, of *Dendrodoris* and *Doriopsilla*.

	Dendrodoris	*Doriopsilla*
Anterior Digestive		
mouth	glandular cells present	glandular cells present
oral tube	uniform width, no glandular development	broad, extensive thick glandular layers
oral glands	distinctly separate ptyaline glands	integral part of oral tube
salivary glands	paired glands with compact follicles	absent
pharynx	Y-shaped lumen, 2 muscle layers, no glandular development, thin cuticle	Y-shaped lumen, thimer muscle layers glandular cells present, thin cuticle
oesophagus	extremely glandular development, 2 muscle layers, no cuticle	not glandular, considerable muscle development, no obvious gland cells
Reproductive System		
distal oviduct	vestibular gland present in some species	no glandular development
ovotestis	intermingled ovotestis, kidney & digestive gland tissue	layered arrangement of ovotestis, kidney and digestive tissue

serial sectioning at 2-4 um thickness. Sections were taken using a powered microtome equipped with a tungsten-carbide knife. The resulting sections were stained for 20 seconds with 1% toluidine blue which had 1% borax added.

Comparison is made with sections of *Dendrodoris nigra* and other dorids (WÄGELE *et al.*, 1999). For information related to the colour forms of *Dendrodoris fumata* the reader is referred to BRODIE *et al.* (1997). For anatomical drawings and a general description of the organ systems of dendrodorids the reader is further referred to VÁLDÉS *et al.* (1996), BRODIE *et al.* (1997), VALDÉS & ORTEA (1997) and GOSLINER *et al.* (1999).

RESULTS

The dendrodorid genera are dissimilar in external appearance (Figure 1A-C). However, the gross anatomy of their anterior digestive systems shows some similarity with respect to the relative position and size of components (Figure 2). Even at this level differences with respect to the form and position of the oral glands and the presence of salivary glands is obvious. Histological examination provided several additional similarities and differences that are detailed below and summarized in Table 1.

Anterior Digestive System

Mouth

All specimens examined of both genera possess similar glandular cells surrounding the mouth. The epithelium consists of high columnar cells. These cells contain large rounded basally positioned nuclei with bluish contents and clumps of small dark purple staining grana.

Oral Tube

In *Dendrodoris* the oral tube is relatively long and uniformly simple. However in *Doriopsilla* it is at first simple but then expands to become relatively broad. In *Doriopsilla* the oral tube also contains thick glandular layers within the tube wall. These glands first appear dorsally but soon surround the entire tube. Close to the mouth the lumen of the tube is small and round but in the broader section before the pharynx it becomes much larger and folded. Although the same extensive glandular development of the oral tube is present in both species of *Doriopsilla* examined, the extent of the exterior muscle layer is variable.

Oral glands

In *Dendrodoris* the paired oral glands (ptyaline glands) are distinctly separate organs connected to the distal oral tube by a thin very muscular duct (Figure 2). Many of the cells contain large pale-staining vacuoles (Figure 1D). In contrast, the oral glands of *Doriopsilla* are not only different in appearance but are an intregal part of the oral tube. The walls of the oral tube are extremely glandular in appearance with large dark-purple staining cells (Figure 1E). The build-up of glands in this section of the digestive system is similar in appearance to that found in the oesophagus of *Dendrodoris*.

Salivary glands

The paired salivary glands of *Dendrodoris albobrunnea*, *D. guttata* and *D. fumata* are found close to the junction of the pharynx and oesophagus. The cells of this gland form compact follicles, which in turn contain small-round blue-staining vacuoles (Figure 1F). No epithelium layer can be seen surrounding the exterior of the gland, however a narrow lumen can be seen centrally. Sparsely scattered throughout the gland are several large cells with granular-looking pink-staining contents. No salivary glands appear to be present in either of the *Doriopsilla* avoid hyphens in generic names if possible examined.

Pharynx

A thick layer of muscle surrounds the pharynx of all *Dendrodoris* examined (Figure 3A). Another thinner muscle layer is found immediately inside the epithelial layer of the distinctly Y-shaped lumen. Glandular cells are lacking and the lumen possesses a thin but distinct cuticle. The cells of the pharynx contain large vacuoles that display an open spongy network-like structure.

Although the same basic external shape and characteristic Y-shaped lumen is repeated in *Doriopsilla*, the structure of cell layers is quite different (Figure 3B). Muscle layers are thimer and some glandular cells

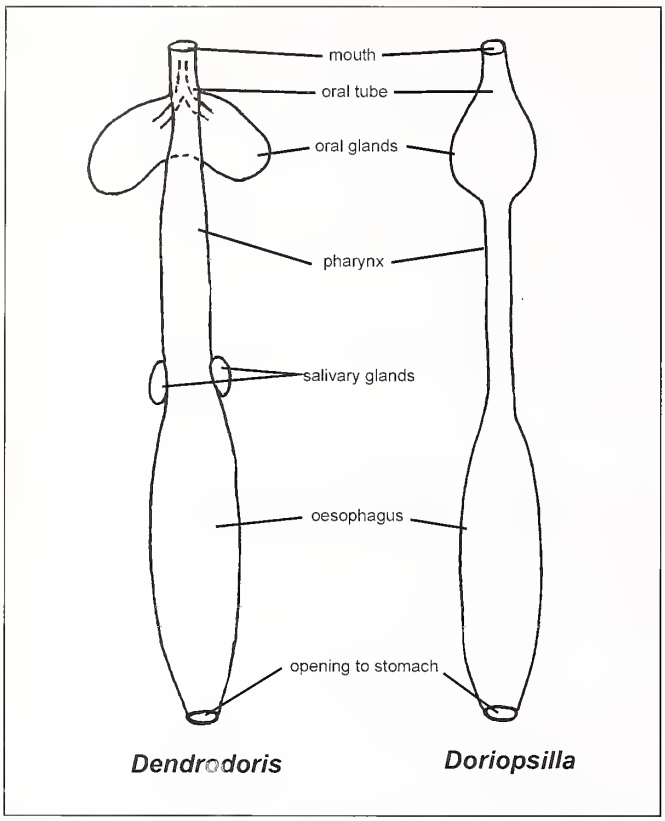

Figure 2. A schematic diagram comparing the anterior digestive system of *Dendrodoris* and *Doriopsilla*.

are present. Some cells with large non-staining vacuoles are present, as is a thin cuticle.

Oesophagus

The oesophagus of all *Dendrodoris* examined is extremely glandular in appearance (Figure 3C). A variable but distinct band of muscle surrounds the outer surface of the organ. There is no cuticle present in the lumen, and in many sections the dark purple glandular development is so extensive that the central lumen is difficult to locate.

The oesophagus of *Doriopsilla* has quite a different cell structure to that found in *Dendrodoris* (Figure 3D). Primarily the oesophagus is not glandular in *Doriopsilla,* but very muscular and the general histological appearance of the organ is quite different to that found in *Dendrodoris.* There are no obvious gland cells present but the muscle tissue is interspersed by cells with relatively large vacuoles containing pink-staining secretions. The oesophagus is surrounded by a very broad but loose layer of circular muscle followed by another broad layer of loose longitudinal muscle. In some areas of the oesophagus radial muscle is also distinctly present. The extent of this radial muscle is variable along the length of the organ. The oesophageal lumen is narrow distally but then widens. The epithelium of the lumen consists of uniform cells with large dark staining nuclei. No cuticle is present.

Reproductive System

Distal Oviduct

The presence of a vestibular gland associated with the distal oviduct varies between species. The gland is present within *Dendrodoris albobrunnea* and *Dendrodoris fumata* (both grey and orange/red forms) but absent in *Dendrodoris guttata*. The presence of microvilli is clearly seen in the gland of *Dendrodoris fumata* but is not so obvious within the gland of *Dendrodoris albobrunnea*. This could be the result of incomplete sexual maturity. In some species (e.g. *D. fumata*) this gland is not visible by dissection because of its position within the connective tissue of the body wall or oviduct. No vestibular gland or microvilli are present in association with the oviduct of either of the *Doriopsilla* examined in this study. The genital aperture and associated ducts are however, often distinctly folded and convoluted.

Ovotestis (Gonad)

In both genera the ovotestis (gonad) is locationally associated with the anterior digestive gland. The relative position of ovotestis, kidney and digestive gland tissue in all of the *Dendrodoris* examined is intermingled (Figure 3E). In contrast, in *Doriopsilla* it displays a more defined layered arrangement (Figure 3F). Thus in *Doriopsilla* the ovotestis forms a compact flattened layer which lies dorsally over the anterior of the digestive gland. In *Dendrodoris* however, the ovotestis forms branched projections, which sit above, below and between the digestive gland follicles and kidney tissue.

DISCUSSION

Anterior Digestive System

The anterior digestive system of the smooth bodied *Dendrodoris guttata*, *Dendrodoris albobrunnea* and *Dendrodoris fumata* is very similar to that already found by WÄGELE *et al.* (1999) for *Dendrodoris nigra*. Like *D. nigra* there is separate paired oral (ptyaline) glands, a network like pharynx, extremely glandular oesophagus and small compact salivary glands.

Oral tube and Oral glands

The oral glands, defined as glands associated with the oral tube, of all *Dendrodoris* examined are paired structures, distinctly separate from but connected to the oral tube by a single muscular duct. The oral glands of *Doriopsilla* on the other hand are found sub-epidermally within the walls of the oral tube itself. According to WÄGELE & WILLAN (2000) the latter arrangement is considered to be the plesiomorphic (primitive) state for nudibranchs.

Salivary glands

Suprisingly, the salivary glands of *Dendrodoris albobrunnea*, *D. guttata* avoid if possible and *D. fumata* are different from that reported by WÄGELE *et al.* (1999) for *Dendrodoris nigra*. Rather than containing large very pale staining cells, superficially similar in appearance to the cells of the ptyaline gland, the salivary glands cells in the *Dendrodoris* examined in this current study are different, being uniform blue in appearance and not containing any very-dark staining nuclei.

According to WÄGELE & WILLAN (2000) salivary glands are absent in only a few nudibranch genera. The presence of relatively compact salivary glands in all *Dendrodoris* examined confirms this character as an autapomorphy for the genus, however this character can no longer be extended to the Dendrodoridae since no salivary glands were found in *Doriopsilla*.

Pharynx

The pharynx (defined as the section of the digestive system between the oral tube and the oesophagus) is uniform in structure within the *Dendrodoris* examined. Histologically the pharynx displays a distinct network-like appearance as previously mentioned for *D. nigra* by WÄGELE *et al.* (1999) and described as homologous to the radula bearing cushions of other gastropods. Recent investigations of

Doriopsilla (GOSLINER *et al.*, 1999; VALDÉS & ORTEA, 1998; VALDÉS & GOSLINER 1999) have not acknowledged the presence of a pharynx, the area being interpreted as the first section of a two-part oesophagus. The similar appearance of this part of the digestive tube in both *Dendrodoris* and *Doriopsilla*, and its similarity to the radula-bearing cushions of other gastropods, is clearly shown by the histological results of this study.

Oesophagus

The histological results indicate that the function of the oesophagus in *Dendrodoris* and *Doriopsilla* is quite different. In *Dendrodoris* this organ is extremely glandular indicating that its primary function lies with the production of digestive fluids. In *Doriopsilla* on the other hand this role is obviously performed by the extremely dense oral glands present in the walls of the oral tube. The notable muscle development of the oesophagus in *Doriopsilla* suggests a more mechanical role in the digestive process. The absence of a cuticle in the oesophagus of both *Dendrodoris* and *Doriopsilla* is expected. According to WÄGELE (1997) an oesophagus without a cuticle is an autapomorphy for the Doridoidea.

Reproductive System

Distal oviduct

The presence or absence of a vestibular gland in the reproductive system, as determined by dissection, has previously been used as a

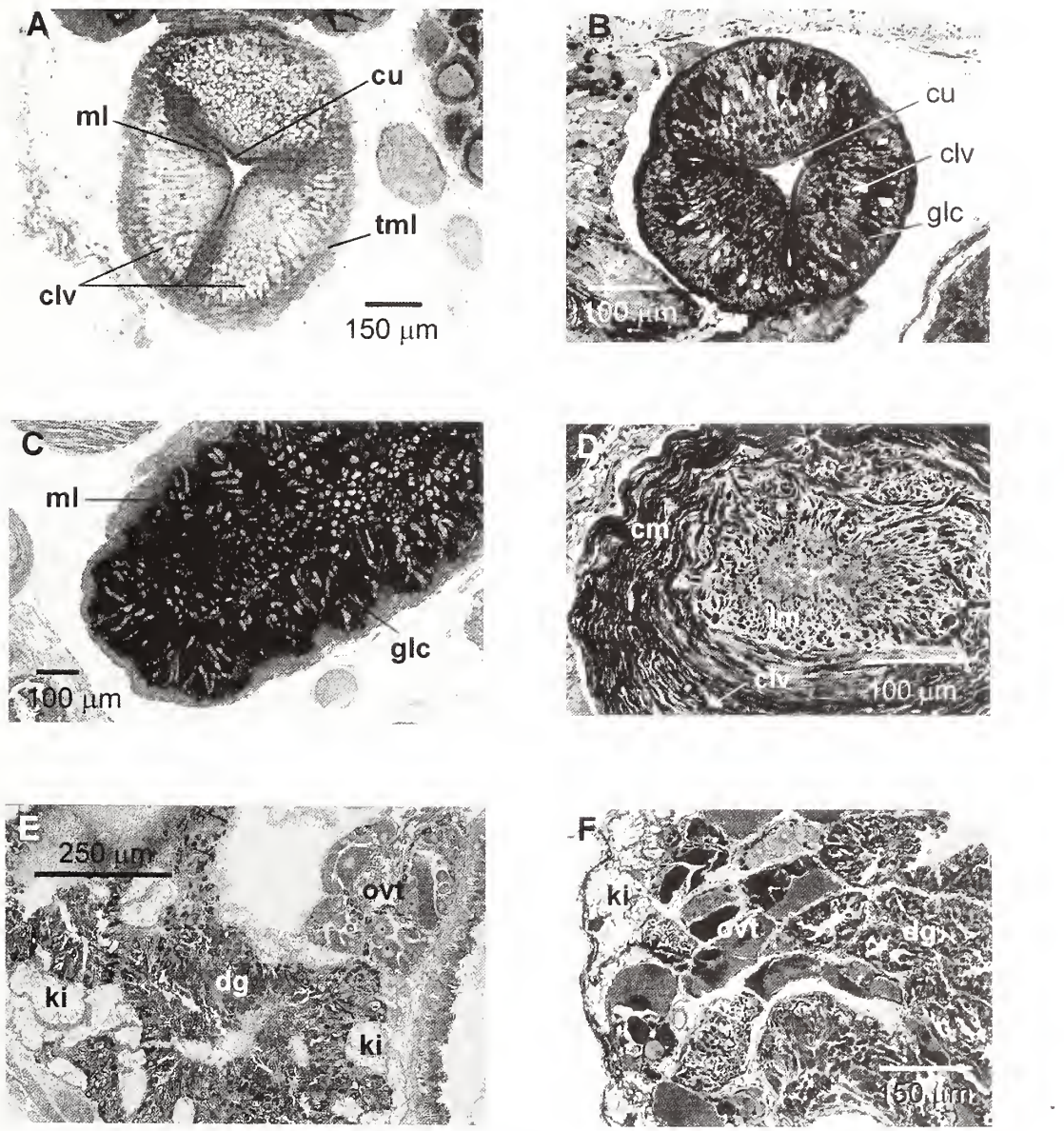

Figure 3. A. A histological cross-section of the pharynx in *Dendrodoris fumata* (grey form) B. A histological cross-section of the pharynx in *Doriopsilla miniata* C. A histological section of the oesophagus in *Dendrodoris fumata* (grey form) D. A histological section of the oesophagus in *Doriopsilla miniata* E. A histological section showing the intermingled arrangement of the ovotestis (gonad), kidney and digestive gland in *Dendrodoris fumata* (orange/red from) F. A histological section of the ovotestis (gonad), kidney and digestive gland in *Doriopsilla miniata* showing a layered arrangement.
Abbreviations: cu = cuticle, cm = circular muscle, dg = digestive gland, glc = gland cell, ki = kidney, lm = longitudial muscle, clv = cell with large vacuole, ml = muscle layer, ovt = ovotestis (gonad), tml = thick muscle layer.

species separating character for dendrodorids (BRODIE *et al.*, 1997). VALDÉS & GOSLINER (1999) in their phylogenetic analysis of radula-less dorids also utilized this character. However, the results of the present study clearly show the need for histological investigation of such characters, since positioning within the body wall or connective tissue can cause the presence of such glands to be consistently overlooked by dissective investigation alone. This is the case for *Dendrodoris fumata*, which until the present study had been thought to lack a vestibular gland.

The lack of glandular development on the distal oviduct of *Doriopsilla* and *Dendrodoris guttata* is noteworthy considering the unique findings of this area in *Dendrodoris nigra*, where thousands of symbiotic bacteria were found in a vestibular gland annexed to the distal oviduct (KLUSSMAN-KOLB & BRODIE, 1999). Results to date indicate that sexual maturity may influence the presence of microvilli and/or bacteria.

Ovotestis (Gonad)

The unusual intermingled position of ovotestis, kidney and digestive gland reported by WÄGELE *et al.* (1999) for *Dendrodoris nigra*, is also found in all other members of *Dendrodoris* examined in this present study. Such an arrangement appears to be unique to the genus. The layered arrangement found in both *Doriopsilla* species examined is more typical of other dorids. These results are in direct conflict with the findings of VALDÉS & GOSLINER (1999) who determined (without histological investigation) that in the majority of *Dendrodoris* species the hermaphrodite gland (ovotestis) was clearly separate from the digestive gland, and that in *Doriopsilla* the two glands were interdigitated.

CONCLUSIONS

The function of the respective components of the anterior digestive system would appear to differ substantially between the two-dendrodorid genera. All *Dendrodoris* characters considered by this study, except salivary gland structure and vestibular gland development, appear consistent across the genus. The study indicates that the continued use of methacrylate resin histology will provide the additional character sets required to adequately address the question of how closely related the radula-less dorid nudibranchs are. Moreover, it highlights the importance of information derived from histological investigations, to both taxonomic and phylogenetic analyses. A very clear example of this is the discovery of a vestibular gland within the reproductive system of *Dendrodoris fumata* that is not visible by dissection. Further studies of dendrodorids are required to investigate all organs systems, examine tuberculate dendrodorids (such as *Dendrodoris tuberculosa* (QUOY & GAIMARD, 1832) and compare (using the same techniques) other radula-less nudibranch families, particularly Phyllidiidae and Tethydidae.

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Some perspectives on the biology and ecology of nudibranch molluscs: generalisations and variations on the theme that prove the rule

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KEY WORDS: Predator-preyassociations; life cycle, life history; reproduction; egg size, poecilogony.

ABSTRACT Aspects of the ecology and reproduction of nudibranch molluscs are addressed in terms of the generalisations often applied to the group. We summarise the present applications of nudibranchs as model systems and highlight their potential for investigating other ecological problems. A commonly held view is that species of the Order are characterised by being specialist predators. The available literature supports this generalisation: approximately 50% of the species of known diet are associated with just one prey species (monophagous) and many stenophagous species probably prefer just one or two species. Even those generalists that prey upon a number of species still are specialised at higher taxonomic levels, in being obligately associated with, for example, only sponges, bryozoans or anemones. With respect to life cycles and life history, we present data for the dorid *Cadlina laevis* which show this species to be unique in the literature in displaying a perennial life cycle, spawning just once per year, and surviving to perhaps 5 or 6 years of age. This is in marked contrast to the typical annual/subannual life cycles and semelparous life history reported for other species. Given the difficulties in undertaking field population studies, we question how representative are the reported species, which form the basis of generalisations for the Order. Intraspecific variation in egg sizes is discussed in terms of empirical data for several intertidal populations of the dorid, *Adalaria proxima*; striking within and between population variation in egg sizes indicates marked differences in larval 'quality', but whether these differences are adaptive, or nonadaptive consequences of genetic drift of closed populations, remains open to further study. The potential evolutionary importance of egg size variation in relation to shifts in mode of larval nutrition from planktotrophy to lecithotrophy also is discussed. The generalisation that this Order also is characterised by simultaneous hermaphroditism is valid, but not without exception. Laboratory studies have shown that *Phestilla sibogae* is functionally male at an extremely small size and that sperm received and stored at otherwise juvenile body sizes are disproportionately successful in fertilising an individual's oocytes; in terms of sperm competition models this is a clear example of first male/partner precedence. Finally, the phenomenon of poecilogony — switching of larval strategies within species populations — is discussed in the light of recent examples amongst nudibranchs and ascoglossans. If a real and widespread (albeit rare) phenomenon, the fuller understanding of poecilogony presents larval ecologists with a considerable challenge.

RIASSUNTO Alcuni aspetti dell'ecologia e delle strategie riproduttive nei molluschi nudibranchi e i modelli funzionali che ne derivano hanno una grande importanza anche per la comprensione di problematiche ecologiche d'interesse generale.
I nudibranchi sono generalmente considerati predatori specialisti: circa il 50 % delle specie studiate è monofago e gli stenofagi predano, di norma, due-tre specie. Le specie generaliste sono inoltre strettamente legate a ben determinati livelli tassonomici siano questi poriferi, briozoi o cnidari.
Il ciclo vitale del doridaceo *Cadlina laevis* sembra essere particolare, presentando una riproduzione all'anno e concludendosi in forse 5-6 anni. Ciò è in contrasto con i tipici cicli annuali o subannuali e la semelparità delle altre specie di nudibranchi. Considerando la difficoltà di condurre ricerche di campo in questo settore questi risultati suggeriscono una certa cautela nel generalizzare i cicli vitali in questo Ordine.
Variazioni intraspecifiche nel diametro delle uova in diverse popolazioni del doridaceo intertidale *Adalaria proxima* induco a pensare che possano esserci differenze significative nella "qualità larvale" in popolazioni diverse; se tali differenze siano adattative o meno, cioè conseguenza di un drift genetico di popolazioni isolate, rimane un problema insoluto. Viene anche discussa l'importanza evolutiva delle variazioni nelle dimensioni delle uova in funzione d'eventuali passaggi da una strategia planctotrofica ad una lecitotrofica.
I nudibranchi presentano, generalmente, un ermafroditismo simultaneo, ma non mancano le eccezioni. Studi di laboratorio hanno dimostrato che individui di taglia molto piccola di *Phestilla sibogae* sono maschi funzionali, ma gli allospermi acquisti a qualsiasi taglia giovanile hanno modeste probabilità di fecondare gli oociti dell'individuo: questo modello di "sperm competition" è un chiaro "first male/partner precedence".
Infine, il fenomeno della pecilogonia – l'eliminazione della fase larvale all'interno di singole popolazioni – viene discusso alla luce di recenti esempi tra nudibranchi e ascoglossi. Se questo processo sia reale, diffuso o, al contrario raro, rimane un importante spunto di ricerca per l'ecologia larvale.

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INTRODUCTION

Experimental biologists have constantly sought species to provide model systems for specific topics of research. Of these, a limited number do become utilised worldwide in certain fields; *Drosophila* and *Caenorhabditis elegans* Maupas are perhaps preeminent examples in genetics and developmental biology. The advantage of one or a few species providing a model for a wide array of research is the knowledge base upon which any new approaches can be built. But one of the consequences is that it perhaps becomes easy to lose sight of the variation that is the very essence of biology. Ecophysiological research on the widely distributed blue mussel, *Mytilus edulis* L., has proven this to be a most valuable model organism both for empirical and modelling studies concerning marine pollution; from this there have developed numerous monitoring programmes successfully deploying molluscs as sentinel organisms in pollution studies (e.g. Mussel Watch programmes, BELIAEFF *et al.*, 1998; CANTILLO, 1998; LAUENSTEIN & DASKALAKIS, 1998). However the benefits of

comparability of responses for a single species at different localities must be weighed against the possible costs of lack of representativeness.

Particular species of nudibranchs have proven to be excellent model species for many aspects of physiological, cell biological and ecological research. Most of these topics are outwith the bounds of the present paper, but particularly prominent examples include:

1. Fundamental neurobiology, and especially neural control mechanisms and central pattern generators; e.g. the escape swimming response of *Tritonia diomedea* Bergh (e.g. WILLOWS *et al.*, 1973; KATZ, 1998),

2. Behaviour and physiology; e.g. the neural basis of associative learning in *Hermissenda crassicornis* (Eschscholtz) (e.g. ALKON, 1984; BLACKWELL & ALKON, 1999),

3. Developmental biology; e.g. the induction and control of larval metamorphosis and morphogenesis in *Phestilla sibogae* Bergh (e.g. HADFIELD, 1977, 1998; HADFIELD & PENNINGTON, 1990).

One objective here is to highlight the further potential that the Order Nudibranchia possibly provides to ecologists as model organisms or systems. Another is to discuss certain aspects of ecological variability, the study of which might prove to be especially tractable with nudibranchs. Third, it is perhaps timely also to reassess the validity of some of the generalised perceptions that are invariably ascribed to this fascinating and varied group of molluscs. When deriving generalisations about the ecology of natural groupings of diverse species, such as the nudibranch molluscs, periodic appraisal should be made of how representative are the studied species, and hence the information base. The degree of dietary specialisation displayed by the four suborders is specifically discussed and the typical life cycles and life history which are held to characterise the order are examined in the light of new data on *Cadlina laevis* (L.).

There are pitfalls in presuming that a single model system explains similar patterns or processes in other species or biotopes. An illustrative example concerning nudibranchs is the remarkable phenomenon of spine elongation as an inducible, adaptive, morphological plasticity amongst bryozoans. HARVELL (1986, 1991, 1998) has undertaken detailed and elegant investigations of the environmental induction of elongate spine formation in colonies of the cheilostomatid bryozoan *Membranipora membranacea* (L.). Elongate spine induction is a phenotypically plastic response by zooids within a colony in mounting a defence against *Paradoridella (=Doridella) steinbergae* (Lance), a specialist nudibranch predator. Induction of spines is rapid (1-2 d) and the response can be elicited by contact with the predator or by waterborne exudates therefrom. Other studies of inducible morphologies for a wide array of invertebrate taxa also reveal the inductive agent to be biological in origin, and commonly attributable to predator species (ADLER & HARVELL, 1990); given that nudibranchs worldwide are major predators of bryozoans it might be expected that other cases of elongate spine induction in bryozoans also will be attributable to predation.

In NW European waters *Electra pilosa* (L.), which also is a member of the family Membraniporidae, is preyed upon by numerous species of nudibranchs and is the preferred diet of several specialists, including the dorid *Adalaria proxima* (Alder & Hancock). Like *M. membranacea*, *E. pilosa* also displays morphs in certain localities with grossly elongated (proximal) spines. From Harvell's work on *M. membranacea* we considered that spine induction in *E. pilosa* possibly was a response to these specialist predators, and perhaps specifically to *A. proxima*. Although predation of *E. pilosa* zooids by *A. proxima* is reduced for long-spined colonies, early field observations did not support this conjecture. Laboratory experiments subsequently confirmed that elongate proximal spines are not induced by *A. proxima*, or other potential predators, but that this plasticity is unique in being induced by an abiotic factor. Induction is only by wave crash-related abrasion of the bryozoan by other macroalgae (BAYER *et al.*, 1997) and wave crash alone would not induce the formation of elongate spines. The partial protection from nudibranch predation afforded to *E. pilosa* colonies by elongate spines is thus fortuitous and this system evidently is quite different to that seen in *M. membranacea*.

The present coverage of topics is deliberately eclectic and not intended to be comprehensive; this is very much a biased perspective of problems of interest regarding particular aspects of their ecology, especially their reproduction, but also we are acutely conscious that these generalisations may not be general at all, but merely reflect personal perceptions or ignorance. Our perspective also is decidedly boreo-centric in that our direct experience of these molluscs in tropical and polar waters is limited and even at temperate latitudes our studies have focused on North Atlantic species and systems.

GENERALIZATIONS PERTAINING TO NUDIBRANCH MOLLUSCS

Despite the considerable morphological and ecological diversity of the Order Nudibranchia, there are embedded in the literature a number of general perceptions about the ecology and biology of the group which perhaps require re-evaluation; if there are marked exceptions to these rules, or if the contentions are not supported by the available empirical data, it is clear that we might be constrained in our perspective. Through our own interests in nudibranchs, we can identify three generalizations or particular features of their biology in this context: these species typically are held to (i) display stenophagous (specialist) prey associations, (ii) to undergo annual/subannual life cycles and to have strictly semelparous life histories, and (iii) to be simultaneous hermaphrodites. Given that nudibranchs are distributed at all latitudes throughout the World Ocean, and occur at all depths from the intertidal to the deep ocean benthos — even at extreme environments such as hydrothermal vents (VALDES & BOUCHET, 1998) — such generalisations obviously require qualification and there are certain to be exceptions. The question is are there sufficient exceptions to warrant reappraisal of the rules?

STENOPHAGOUS PREY ASSOCIATIONS

The term "specialisation", as a categorisation of a species' dietary association(s), is a value judgement and open to various interpretations. As a basis for illustrating ecological trends throughout the Nudibranchia, we here have subjectively categorized all monophagous (single prey species) and stenophagous (2 or 3 prey species) nudibranchs as being "specialists". McDONALD & NYBAKKEN (1997) undertook the considerable task of appraising all the primary sources published prior to 1996 on the recorded diets of nudibranchs throughout the World Ocean. From their database the diets of 600 species representing all four suborders have been extracted. A few species were deleted because of the lack of taxonomic rigour or sufficient detail in the reported dietary species; for example, the only dietary information for *Ceratosoma trilobata* (Gray) is "sponges", whereas *Hypselodoris capensis* (Barnard) is recorded only as preying upon a "light blue sponge". *H. capensis* may well be a specialist predator of only a single unidentified sponge species, but such data were considered inadequate for inclusion; similarly imprecise records for other nudibranchs preying upon multiple taxa were excluded from those particular species' dietary lists. Truly generalist predators, such as the species of *Bathydoris* (benthic carnivores) and *Melibe* (planktivores), also mostly were excluded because of lack of specific detail which would make comparisons problematic. However the rather more detailed information for *Melibe leonina* (Gould) and *Tethys fimbria* (L.) did permit their inclusion with a conservative number of prey taxa set at 10. Records of spurious diets for species observed in captivity also were removed, as were several instances of known synonomy of dietary species (e.g. *Anemonia viridis* (ForskŒl) =*Anemonia sulcata* (Pennant)). Fish eggs (e.g. for *Calma glaucoides* (Alder & Hancock)), and nudibranch eggs (e.g. for *Favorinus branchialis* (Rathke)), were included here as a single dietary 'species' for those nudibranchs, irrespective of the species identity of the spawn. These alterations were, however, minimized in order to preclude personal subjectivity and overall the presented summary illustrations are almost identical to the sources reviewed by McDonald & Nybakken.

As outlined by McDONALD & NYBAKKEN (1997), numerous problems are presented here in terms of the reliability of the primary information. In many senses modern biologists are prisoners of the past, in that there is an obligation to rely upon the veracity of the reported dietary species and correct identifications. Difficulties also inevitably will arise from (historically generalist) species subsequently being split by taxonomists into a grouping of closely related but distinguishable specialists; but these problems are not insurmountable, so long as the original identifications were correct and reported in sufficient detail. The converse problem, of several apparently specialist species being subsumed into a single taxon is less acute. Intractable cases perhaps are best illustrated in the British Isles by *Doto coronata* (Gmelin), a common dendronotid predator of hydroids. *D. coronata* was for long recognised as being widespread and morphologically variable. In occurring both intertidally and sublittorally, and occupying a considerable geographic range, it is to be expected that numerous species would be recorded as its diet. The data include almost certain incorrect attributions (e.g. the ctenostomatid bryozoan *Alcyonidium*), but the overwhelming majority of observations undoubtedly are correct. Only comparatively recently (LEMCHE, 1976; MORROW *et al.*, 1992) have specialist taxonomists commenced the task of differentiating morphologically distinct species within the complex "*Doto coronata*" that in the past certainly have been confused by numerous observers (ourselves included), and who are not taxonomists. It presently is impossible to confidently ascribe the true diet of *D. coronata* and even LEMCHE (1976) was uncertain as to whether or not *D. coronata* should remain a distinct species. Are, for example, all the records of *D. coronata* preying upon *Kirchenpaueria pinnata* (L.) attributable to the separation by LEMCHE (1976) of the specialist predator of that hydroid, *Doto dunnei* Lemche? The answer almost certainly is yes, but for the present the historical literature for the diet of *Doto coronata* places this species amongst the most generalist of nudibranchs world-wide.

Other than individual researchers making subjective judgements and deletions from prior records and thereby re-writing history, there is no reliable means of expunging even obviously fallacious observations from the literature. The possibility always will remain that *Acanthodoris pilosa* can consume a poriferan sponge, but *A. pilosa* is undoubtedly a specialist predator of ctenostomatid bryozoans. Similarly, the dietary records of cheilostomatid and ctenostomatid bryozoans, octocorallians and "dead fish" for the specialist barnacle predator, *Onchidoris bilamellata* (L.) undoubtedly are invalid. In adopting a conservative approach to the published data it is acknowledged that here only broad patterns which are robust and clear should be deduced. For the above reasons it also is apparent that the data do not warrant detailed statistical analysis, though some simple tests are included below to allow objective testing of general hypotheses and generalisations.

The frequency distribution of the number of dietary species for the 600 species of nudibranchs of known diet (Fig. 1) shows a clear overall pattern, despite the foregoing qualifications. Most obviously, 50% (298/600) of the species are recorded as preying upon a single species and 75% (454) as being associated with only 1-3 prey species. Given that the different suborders are primarily predators of rather different epifaunal taxa (e.g. Doridacea on especially sponges and bryozoans; Aeolidacea on cnidarians), it is notable also that the species of the four suborders show strikingly similar frequency distributions and degree of overall specialisation. Fisher's Exact Test shows no significant difference ($p = 0.352$) in the proportions of monophagous specialists among the four separate suborders. None the less, in terms of the generalisation regarding specificity of diet across the Order, it is important to note that half the species — for which there are data available — do apparently prey upon more than a single species.

But further care is necessary because the very nature of species listings is that the observations are qualitative and unweighted — that is, a single observation for one species cannot be quantitatively evaluated against multiple records of another species or against several different dietary species.

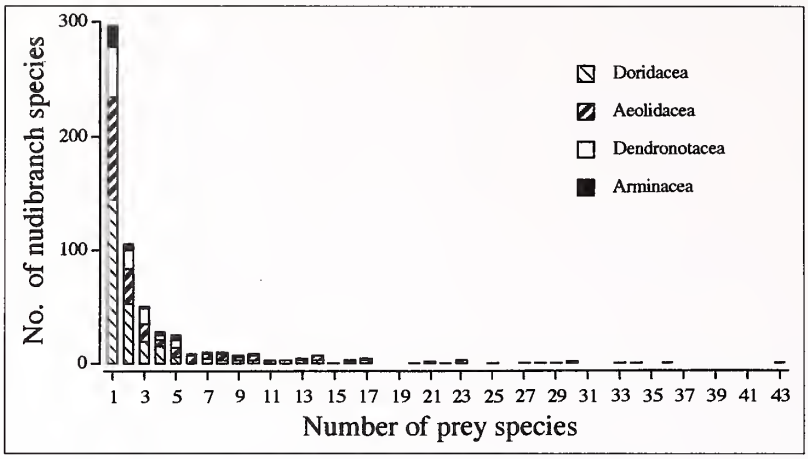

Fig. 1. Frequency distribution of numbers of dietary prey species for 600 nudibranch species (data from McDonald & Nybakken, 1997).

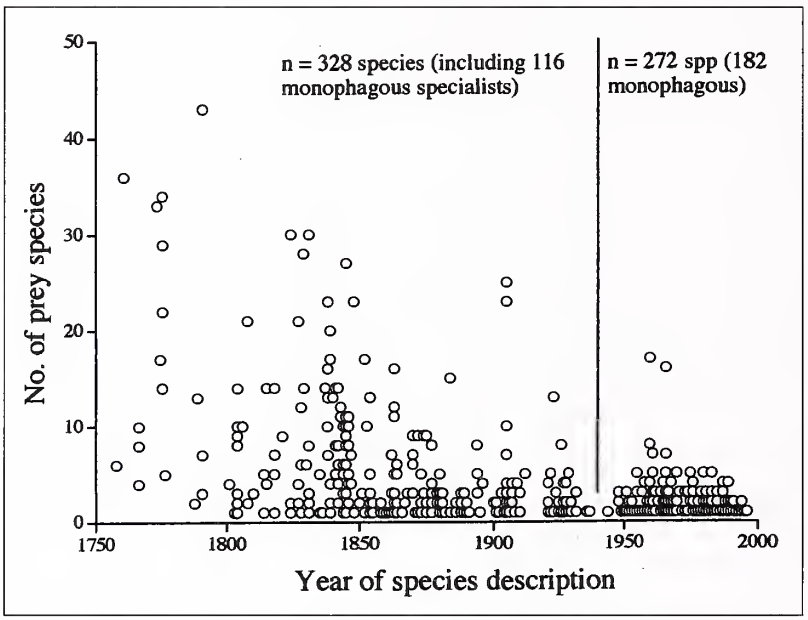

Fig. 2. Scatterplot of the numbers of reported prey species for each of 600 nudibranch species (data from McDonald & Nybakken, 1997) in relation to the year of their description. Monophagous specialists are recorded as preying upon one species only. The data were arbitrarily split into two groupings — those described pre-1937 and those post-1944 — for further analysis.

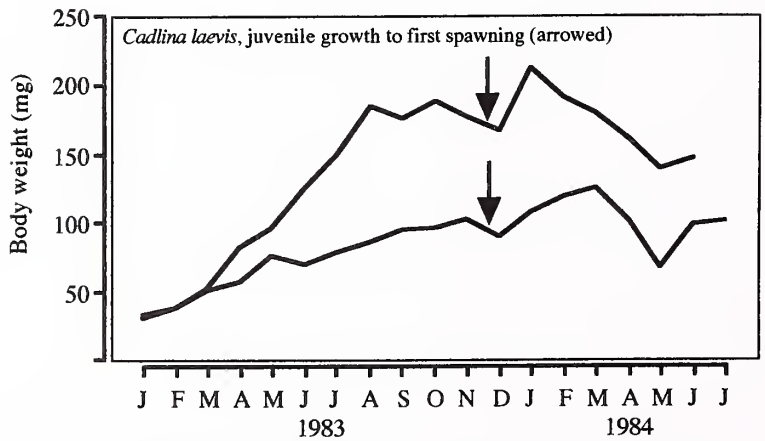

Fig. 3. *Cadlina laevis*. Growth of two example juveniles collected from the field in November 1982 and first weighed in January 1983; these would have hatched from the spawn mass ~April/May 1982. Both spawned for the first time in November 1983, at a benthic age of ~19 months.

According to the published records many specialist nudibranchs probably can exploit several prey species, but the likelihood is that many or most are clearly associated with, or prefer, just the one species (see, for example, MORROW *et al.*, 1992, on *Doto* spp.). In the British Isles *Adalaria proxima* is undoubtedly a specialist predator of the cheilostomatid bryozoan *Electra pilosa*; but it is not monophagous. From extensive field and laboratory observations we have recorded *A. proxima* occasionally feeding on *Callopora lineata* (L.) and very rarely on the ctenostomatids *Alcyonidium gelatinosum* (L.) (Syn. *A. polyoum* (Hassall)), *Alcyonidium hirsutum* (Fleming) and *Flustrellidra hispida* (Fabricius). Other examples of specialists which apparently are associated with (and cryptically camouflaged on) the one prey species in the British Isles include *Tritonia hombergi* Cuvier (on *Alcyonium digitatum* L.), *Tritonia nilsodhneri* Marcus (on *Eunicella verrucosa* (Pallas)), *Cuthona nana* (Alder & Hancock) (on *Hydractinia echinata* (Fleming)), *Onchidoris inconspicua* (Alder & Hancock) and *Onchidoris sparsa* (Alder & Hancock) (on *Cellepora pumicosa* (Pallas)), and *Onchidoris depressa* (Alder & Hancock) (on *Schizomavella linearis* (Hassall)): records do, however, exist of one or more additional dietary species for all of the latter nudibranchs (TODD, 1981).

Despite the frequency distributions for the four suborders being closely similar, there is one clear example of within-group heterogeneity which perhaps warrants closer scrutiny. The family Chromodorididae shows a significant difference (Fisher's Exact Test, p = 0.018) from other non-chromodorid Doridacea in the level of their apparent specialisation: 46 of the 70 reported chromodorids are monophagous, in contrast to only 100 out of 205 non-chromodorids. Do chromodorids differ fundamentally from other families within the Order? The Chromodorididae is essentially a tropical/sub-tropical family (RUDMAN, 1977) and these dorids typically are specialist predators of encrusting sponges. Notwithstanding the possibility that this family truly does show unusually subtle niche differentiation and a high level of dietary specialisation, other factors also might explain their seemingly anomalous status. Many of these species occur in biogeographic areas that are taxonomically relatively poorly-known and many chromodorids seemingly are relatively rarely recorded. Such cases inevitably will appear to be dietary specialists if the nudibranch species, or its diet, have been recorded for example only the once.

An alternative explanation might be that the dietary species are relatively poorly known for this family and thus the (few) attributable records convey the erroneous impression of stenophagy or even monophagy. Many chromodorids can be found actively preying upon sponges in the field, but commonly they are found either cryptically concealed or moving actively across the substratum and not associated with a particular prey organism. Dietary data from observation alone are therefore likely to be sparse. Scuba diving and submersible equipment have been available to biologists for only a relatively short period of time and direct and detailed *in situ* observations of sublittoral nudibranchs active in their natural habitat are therefore relatively limited and recent in a historical context. This constraint in the data has to be viewed in the knowledge that taxonomic descriptions of nudibranchs date back to the application by Linnaeus of the binomial system to animals in 1758 (*Doris verrucosa* Linnaeus).

The historical context is important also in that additions to the listings of nudibranch dietary species (both correct and incorrect) are cumulative in the literature. It is to be expected that species described in the 18th and 19th centuries will by now generally have been reported as having more dietary species than will more recent discoveries and descriptions, unless the former are genuine monophagous specialists and published data are error-free. Fig. 2 shows the recorded number of dietary species in relation to the year of first description of the 600 nudibranch species. Whilst many monophagous specialists were first described during the 19th century, relatively fewer generalist species have been described more recently, although the dietary data for many recently described species probably are as yet incomplete. A comparison of the relative proportions of monophagous to non-monophagous nudibranchs described pre-1938 *versus* post-1943 (Fig. 2) shows a highly significant difference (Fisher's Exact Test, p <0.0001). To an extent this probably reflects better current knowledge both of the predators and their actual and likely (or unlikely, e.g. "dead fish" or "dead anemone") prey items, as well as more rigour (e.g. MILLER, 1961) in the attribution of an organism as a dietary species for a given predator. The recent description of an apparently disproportionate number of specialists is not attributable to large numbers of new descriptions of (monophagous) chromodorids — only 17 of the 46 monophagous chromodorids were described post-1943. The most likely explanations are that (i) insufficient time has elapsed for the full dietary spectrum of some recently described species to be completed, (ii) there is improved scientific rigour in the identifications, observations and interpretations of nudibranch diets, and that (iii) genuinely specialist (monophagous) species are tending to predominate in the recent descriptions.

Monophagous predators can, by definition, display a distributional range only coincidental with that of their single prey species. But the possibility remains for functional monophagy of a stenophagous predator occupying a wide geographic range and exploiting different single species in given areas within that range; the outcome for that species would be for it to appear (in compilations such as the present) a relatively non-specific predator. Some chromodorids display a very wide geographic distribution (e.g. throughout the Indo-west Pacific); over such large distributional ranges it is perhaps inevitable that some apparently specialist, but widespread, predator species will have to exploit various prey species (e.g. the aeolid *Phestilla sibogae* on various species of *Porites*).

As knowledge improves of previously under-recorded areas — such as polar waters, the deep sea benthos, hydrothermal vents and coral reefs of oceanic islands — the world list of described species and their diets will inevitably increase. The more generalist predators will, in all probability, be the more widely distributed, perhaps the more common and thus the most easily found. Commonly found (generalist) species will tend to have the longer taxonomic history. In traditionally

long-researched and well described biogeographic areas, such as the coastal British Isles, recent descriptions are predominantly of monophagous or stenophagous specialists. The third of these possibilities therefore is of especial interest from the wider ecological perspective if it reflects covarying traits of rarity and specialism of diet amongst the Order as a whole. Because this Order includes such a wide variety of epifaunal predators, often preying upon numerically and structurally important epifaunal species within the community (e.g. long-lived anemones and octocorallians), they must offer ecologists considerable possibilities for empirical research on niche breadth, species abundance patterns and predator-prey dynamics (e.g. 'top-down' versus 'bottom-up' control in communities).

Despite the limitations of the data, the conjecture that the nudibranchs as a predatory group are characterised by species with marked dietary specialisations is tenable. Of course many of the seemingly generalist (polyphagous) species in Figs 1 and 2 prey upon multiple species within a single taxon (e.g. Porifera); therefore, at the higher taxonomic levels even these species undoubtedly remain specialised. But as with all ecological patterns there are clear exceptions; some species, such as *Hermissenda crassicornis* (AVILA *et al.*, 1998) and species of *Bathydoris* (WÄGELE, 1989) and *Melibe*, evidently are very much generalists in taking a heterogeneous array of benthic and planktonic prey items. Other species are irrefutably specialists in taking only a particular kind of prey and yet are relatively non-specific within that constraint (e.g. *Aeolidia papillosa* (L.) on anemones). Yet others eat one species only. Specialisation of diet thus remains a subjective judgment, but arguably is a feature that can be extended to the group as a whole.

LIFE CYCLE AND LIFE HISTORY VARIATION

Whereas useful data on the diet of nudibranch molluscs can effectively be compiled from short-term, incidental or anecdotal observations, similar information on longevity, life cycle and life history can be reliably attained only by extensive and repeated field and laboratory observation. Most nudibranchs are relatively small-bodied and quite probably are relatively short-lived. Many species, and most particularly those from higher latitude waters, typically are strongly seasonal in their occurrence and/or spawning activity. But in appraising the generalisation of their typically having annual/subannual life cycles, probably the greatest problem lies in assessing how representative of the Order are the species upon which published studies are available. Practically, long-term quantitative studies are constrained by the species being of suitable abundance or density and of consistent abundance over numerous seasons or years. Such studies for particular localities (e.g. EYSTER, 1980) or biotopes within localities (e.g. kelp epibionts; LAMBERT, 1991) are remarkably few in number and even then are typically restricted to a maximum of perhaps only 2 to 3 years duration. Given that species rarity is the ecological rule, the question has to be asked whether or not published studies have concerned the "sparrows", or the striking exceptions to the rule, within the Order Nudibranchia.

Strictly defined, semelparous organisms undergo a single spawning event, as exemplified by some epitokous polychaete species in which the body wall ruptures on release of the gametes. Nudibranchs typically produce several spawn masses during a single reproductive season, perhaps of a few weeks or months duration, and copulate repeatedly between spawnings. Semelparity commonly covaries with such demographic traits as restricted longevity. Iteroparity, by contrast, concerns repeated and discrete spawning events or reproductive periods which are separated by a quiescent phase of gonadal regression, and this strategy commonly covaries with extended longevity. Nudibranchs can be considered semelparous (despite spawning repeatedly) in that having once attained maturity their period of spawning is inevitably followed by genetically programmed post-reproductive death. Spawning may be delayed by the absence of copulation but infertile spawns still are produced and the animal dies. Observations of the boreo-Arctic chromodorid *Cadlina laevis* (L.) have, however, shown that this species is very much an exception to other published studies.

Cadlina laevis may attain 30-40mm in mantle length (up to ~260 mg live weight). This species is very unusual in undergoing true 'direct', nonpelagic embryonic development (THOMPSON, 1967): most cases of nonpelagic development in nudibranchs concern the shelled lecithotrophic veliger undergoing metamorphosis within the egg capsule (capsular metamorphosis) or soon after hatching. Embryos of *C. laevis* do not develop into a veliger as such and have only a transient and vestigial larval shell. Embryonic development results in a fully-formed benthic juvenile of 0.8-1 mm length hatching from the egg capsule. This species occurs both intertidally and sublittorally, is widespread in the North Atlantic and is most common in the British Isles on northeastern coasts. Spawning on the east coast of Scotland occurs in winter and, somewhat paradoxically, small intertidal juveniles (<10 mm) are found co-occurring in autumn with adults (~20-40 mm) that are approaching maturity, as indicated by the well-developed ovotestis clearly visible through the dorsum. Within the constraints of the above generalities on nudibranch life histories, two possible explanations appear most likely. First, this species might be annual in life cycle, but spawn aseasonally; alternatively, the life cycle actually might be biennial, with individuals reproducing only in their second year. Biennialism as a life cycle strategy is rare in both plants and animals, although several British nudibranch species are known to be biennial and semelparous, including *Archidoris pseudoargus* (Rapp), *Jorunna tomentosa* (Cuvier) and *Tritonia hombergi*. The latter three species all are notable in being relatively large and preying upon stable prey resources (e.g. *Archidoris pseudoargus* on the sponge *Halichondria panicea* (Pallas)) which are predictably available year-round.

Cadlina laevis is a predator of slime sponges and laboratory observations indicate this to be a specialist on *Halisarca dujardini* Johnston which also persists year-round; individuals can be maintained throughout the life cycle on *H. dujardini* alone, but in the field it is seldom associated with any prey organism. The laboratory maintenance of 10 juvenile individuals (4-5 mm at collection in autumn) reared under ambient temperature (3.5-20°C) and photoperiod in through-flow aquaria over 3.5 years,

revealed the growth of this species to be extremely slow (Fig. 3). Respirometric data showed low metabolic rates which, in contrast to the strictly annual *Adalaria proxima* and the biennial *Archidoris pseudoargus* (Rapp), were relatively insensitive to temperature (Fig. 4). Composite data for 28 *C. laevis* also collected in the autumn, but as larger individuals, ongrown in the laboratory for 3.5 years (Fig. 5) not only confirmed the slow growth and extended life cycle, but demonstrated that reproduction first occurs when individuals are ~1.5-2 years old. Annual reproductive effort (turnover ratio; HAVENHAND & TODD, 1988b/1989) and fecundity both are low (32%; 10^2-10^3 eggs, respectively) and packaged as a single spawn mass in any one year. Adults survive after spawning and may well spawn once per year another two or three times and attain an age of 5-6 years. Furthermore, many individuals showed a very atypical pattern of post-spawning somatic growth, compared to annual species (e.g. *Aeolidia papillosa* (HALL & TODD, 1986), *Adalaria proxima* and *Onchidoris muricata* (HAVENHAND & TODD, 1988a, 1989)), in attaining a midsummer peak in size followed by a decline towards spawning in the subsequent winter. The body sizes of individuals in their later spawning seasons often were smaller than the maximum achieved during the second year of life (e.g. Fig. 5). Thus, other than allowing the distinguishing of young 0+ juveniles, body size is a totally unreliable indicator of age in this species which is atypical in displaying both a perennial life cycle and iteroparity.

Given that generally little is known of the reproductive strategy of most species of nudibranch, other than perhaps egg sizes and larval type (e.g. HADFIELD & SWITZER-DUNLAP, 1984; HADFIELD & MILLER, 1987), these data for *Cadlina laevis* suggest that caution should be extended in presuming that nudibranch species conform to the preconception or generalisation of invariable annual/sub-annual life cycles and semelparity. Extended life cycles and iteroparity may be far more widespread traits among those species which are insufficiently common for quantitative population analysis in the field, or for which laboratory rearing has not been attempted or proven possible. Although adult size alone is not a reliable indicator of either life cycle or life history, the likelihood is that especially other large-bodied nudibranch predators of sponges in the British Isles (e.g. *Geitodoris planata* (Alder & Hancock)) and elsewhere also are longer-lived biennials or perennials, and that iteroparity may yet be comparatively widespread in both tropical and temperate waters.

EGG SIZE VARIATION AND LARVAL TYPE

HADFIELD & MILLER (1987) reviewed the egg sizes of opisthobranch molluscs. Amongst the difficulties they encountered were different authors reporting different egg sizes for the same species and instances of the same author(s) reporting different egg sizes for the one species in different studies. Despite this, their compilations have proven very valuable in allowing interpretations of broad patterns of distributions of egg sizes in relation to the different larval developmental types within both the Nudibranchia (250 spp) and the Opisthobranchia in general (369 spp). Reproductively active nudibranchs often spawn within a few hours of retrieval to the laboratory irrespective of whether or not they are maintained on their dietary species; this behaviour is convenient for the compilation of egg diameter measurements and permits the likely assumption that the reported species provide an unbiased sample of the Order. HADFIELD & MILLER (1987) showed that most nudibranch species have planktotrophic larvae which hatch from relatively small eggs (zygote diameter range ~50-170µm; mode ~75µm). Nonpelagic lecithotrophic species display the largest eggs (range ~100-380µm; mode ~205µm), with pelagic lecithotrophic species generally intermediate (range ~100-220µm; mode ~135µm).

Despite the uncertainties of the precision of the data (HADFIELD & MILLER, 1987), these patterns are both clear and conform to expectations of relationships between egg size and larval type in other groups of marine invertebrates (JABLONSKI & LUTZ, 1983; GRAHAME & BRANCH, 1985; HAVENHAND, 1995; WRAY, 1995; MCEDWARD & JANIES, 1997; PECHENIK, 1999). But given that HADFIELD & MILLER (1987) utilised only mean values it is of interest also that there is considerable overlap of the data, in that the largest reported planktotrophic egg size (~165µm) also is firmly within the range more typically associated both with pelagic and nonpelagic lecithotrophic development. If nothing else, this is persuasive in showing that planktotrophic nudibranchs are not subject to selective pressures to minimize egg size (and hence maximize egg numbers) (see also MCEDWARD, 1997). Setting aside the possibilities of additional embryonic resource provisioning by extrazygotic yolk (a feature widespread amongst ascoglossans; BOUCHET, 1989), if one allows that (i) lecithotrophy demands more reserves per embryo and (ii) that there is a general evolutionary progression from (primitive, ancestral) planktotrophy towards (advanced, derived) lecithotrophy (e.g. STRATHMANN, 1985), it follows (iii) that egg size increases are an essential requirement in the evolution of lecithotrophy (KEMPF & TODD, 1989). The implications are, however, that there is a minimum egg size (~55µm) below which the nudibranch larval form cannot be supported.

From Hadfield & Miller's data it is obvious that egg size alone is not the sole determinant of larval strategy, although lecithotrophy is seemingly not supportable by egg sizes characteristic of most planktotrophic species (50-100µm). Lecithotrophic development differs fundamentally from planktotrophy in many ways other than the embryo simply developing from a larger egg. Larval swimming and food capturing organs differ between the two, as do structures of the gut and the capacity for larval feeding; note also that despite being carnivorous as adults, these planktotrophic larvae are essentially consumers of particulate plant material and this will require biochemical and morphological changes in gut structure through metamorphosis (BICKELL *et al.* 1981; KEMPF & TODD, 1989; TODD, 1991). The levels of ontogenetic development at hatching also differ markedly, especially in the development of foot musculature and the larval sensory systems. At hatching, planktotrophic larvae of nudibranchs have no propodium and generally lack eyes, though there are some exceptions to the latter (HIRANO & HIRANO, 1991), whereas all lecithotrophic larvae

have a well-developed foot and eyes at hatching. Thus, although a component pre-requisite for support of lecithotrophic development, a larger egg does not simply confer transition from planktotrophy to lecithotrophy.

INTRA-SPECIFIC VARIATION IN EGG SIZE: ARE ALL EGGS EQUAL?

Although compilations such as those of HADFIELD & MILLER (1987) are valuable in revealing general trends and patterns in the development of opisthobranchs, allowance cannot be made for intraspecific variation in egg size. There is no reason to suppose that egg size as a trait should be fixed for any one species. Here we ask the questions; to what extent does egg size vary within species, and does such variation have adaptive potential? The focus of our studies has been *Adalaria proxima*, a common dorid which is widely distributed throughout the northern British Isles. Its range includes NE England, all of Scotland, N Wales and N Ireland. It is strictly annual in life cycle and reproduces by means of pelagic larvae. Metamorphosis is induced by a water-soluble moeity derived from the prey bryozoan, *Electra pilosa* (LAMBERT *et al.*, 1997), but never occurs within the capsule. The larvae can feed (KEMPF & TODD, 1989) but do not have to feed to complete metamorphosis and they thus are categorised as pelagic lecithotrophic. Post-spawning mortality of adults is absolute and recruitment of the subsequent generation is from pelagic larvae.

Although the dispersal potential of this species is not as high as sympatric planktotrophic counterparts (e.g. *Goniodoris nodosa* (Montagu), TODD *et al.*, 1998), laboratory observations suggest that a pelagic life of several days is not unusual, and delay of metamorphosis may extend to >2 weeks. Adult *Adalaria proxima* were sampled for the 1993-94 generation from five inter-

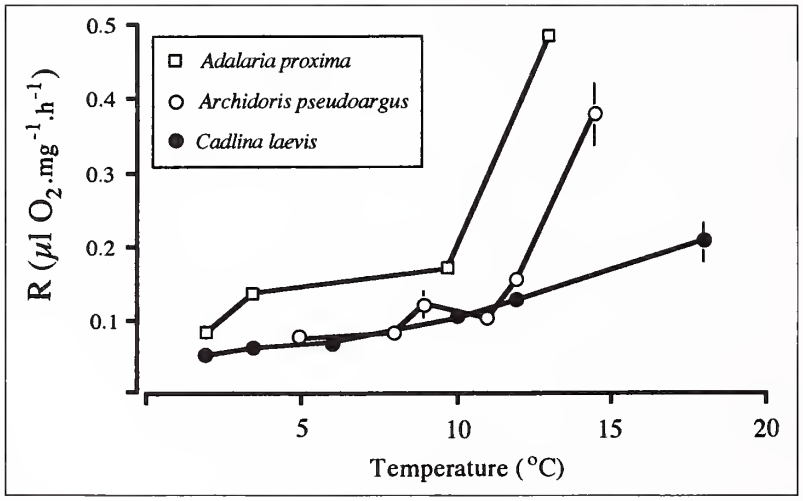

Fig. 4. Respiration rates (R, weight specific consumption of oxygen), over the seasonal temperature range, for the annual semelparous dorid *Adalaria proxima* (data from HAVENHAND & TODD, 1988a), the biennial semelparous *Archidoris pseudoargus*, and the perennial iteroparous *Cadlina laevis*. *Cadlina laevis* shows relative insensitivity to temperature. Error bars for *A. pseudoargus* and *C. laevis* are ± s.e.

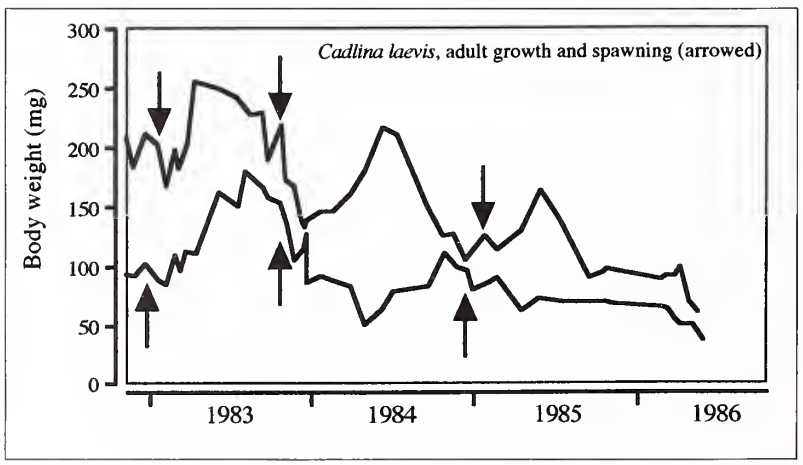

Fig. 5. *Cadlina laevis*. Growth and spawning of two example adults first collected in October 1982. Each spawned once only in each of three successive winters over ~3.5 years in the laboratory and probably were 5 or 6 years old at death. Note that annual spawning did not coincide with peak weight in that year and that there was progressive degrowth with age.

tidal locations embracing that geographic distribution. A total of 184 adults were collected just prior to spawning and Fig. 6 shows the mean egg (zygote) diameter measured for 159 spawn masses laid in the laboratory: only those spawns which had yet to commence cleavage could provide the required egg size data. The observed mean range of 149-192µm is considerable, resulting in the larger eggs having 214% the volume of the smaller. Particularly striking is the between-population variation and the consistent pattern of within-population variation in egg size. Assuming that water content and biochemical provisioning of those eggs are proportionally similar, it is evident that all eggs are not equal and that in the extreme some embryos have more than double the reserves of others.

The implications for this on size and 'quality' of embryos are obvious and these differences may well be reflected in similar variation in larval size and 'quality' in terms of metamorphic success, size at metamorphosis and post-settlement growth potential of the juvenile. Such differences in egg size may therefore exert cascading adaptive influences on fitness of individuals. Alternatively, this between-population variation may simply reflect differing environmental conditions (e.g. local habitat variation in abundance of prey bryozoans), because those adults were collected from the different field locations having almost completed their pre-reproductive growth. In August 1992 post-metamorphic juveniles (1-2 mm mantle length) had been sampled for the 1992-93 generation from five sites, including Portaferry and Menai Bridge. The 1992-93 juvenile populations all were reared for 9+ months to spawning (Fig. 7) in the laboratory under identical (field ambient) temperature and photoperiod conditions. Mean egg sizes for the two illustrated Menai Bridge populations showed no significant difference between years (180µm, n = 49 spawns, 1992-93; 181µm, n = 21 spawns, 1993-94; t = 1.206, P = 0.232), but there was a significant difference for Portaferry (162µm, n = 87, 1992-93; 157µm, n = 21, 1993-94; t = -6.353, P <0.001) (Figs 6, 7). Given the small sample sizes for 1993-94 some discrepancy might be expected but, notwithstanding the between-year difference for Portaferry, there is a clear consistency of the between-habitat contrasts for these (and other) sample sites. Because the 1992-93 populations were reared from early post-metamorphic juveniles, under identical conditions and fed to excess, we are confident that these between site differences in egg sizes are largely genetically determined (LAMBERT *et al.*, 2000).

The data in Figs. 6 and 7 are for groups of individuals from the respective populations. Previous analyses (JONES *et al.*, 1996) have shown that individuals' first-laid spawn masses generally are the biggest clutches and also include their largest eggs. Later spawnings typically are of smaller clutches of smaller diameter eggs. Again, assuming that egg volume is a direct measure of embryonic provisioning by the adult, later-produced eggs are likely to be of lower 'quality' than those spawned earliest. Estimates of fecundity, as indirect measures of individual fitness, such as those that we have undertaken in the past (e.g. TODD, 1979; HALL & TODD, 1986; HAVENHAND & TODD, 1988b) probably are therefore quite inappropriate if these egg size differences do indeed reflect differing quality of offspring.

All eggs are not equal, and this reflects ecological variance which is of considerable potential importance. But is this variation adaptive? Do larger eggs give rise to larger, higher quality larvae which have better survival through metamorphosis, and do those larger metamorphs give rise to larger, fitter reproductive adults? Laboratory culture of sampled populations maintained throughout their benthic life to spawning (LAMBERT *et al.*, 2000) showed no simple between-population pattern of reproductive strategy. Each of the five populations investigated appeared to display a unique combination of the following traits; individual growth rate, typical size of spawning adults, egg size, number and size of spawn masses, duration of spawning period, overall reproductive effort and capsular development time for larvae (JONES *et al.*, 1996). These patterns were consistent within populations and it remains uncertain as to whether these differences are attributable to local habitat selection or to neutral effects attributable to random genetic drift of essentially isolated populations. Presently, however we lean to the latter explanation (LAMBERT *et al.*, *op. cit.*) because of the clear and temporally predictable patterns of genetic differentiation of *Adalaria proxima* around the British Isles (TODD *et al.*, 1998); these are indicative of essentially local larval colonisation of pelagic larvae within demographically closed populations.

Restriction of between-population gene flow for *Adalaria proxima* is indicated by the very high degree of differentiation between discrete field populations separated by distances of only a few hundreds or thousands of metres in localities subject to intense tidal currents of up to ≥3 m s^{-1} (TODD *et al.*, 1998). Measures of between-population genetic differentiation for *A. proxima* are of the level more typical of nonpelagic lecithotrophs (TODD *et al.*, *op. cit.*). Larval dispersal therefore appears to be minimal in *A. proxima*, despite laboratory observations of larval longevity indicating that the pelagic lecithotrophic veliger has the potential to disperse considerable distances and to confer at least moderate levels of gene flow between populations. This is presumed to result from behavioural adaptations preventing larvae from entering the water column: those that do become entrained in the water column essentially are lost but longer distance colonisation of new habitats must still very occasionally occur.

Variability in individual larval behaviour may be crucial in this context, in that developmental variability within or between clutches may confer variation in swimming behaviour and thence dispersal/colonization potential. Such variability may be driven by differences in egg size (Fig. 6), and hence the resources provisioned to larvae, and vary both between and within populations and individuals over their spawning lifetime. Certainly, that the larvae of *A. proxima* can feed, but do not have to feed to complete metamorphosis (KEMPF & TODD, 1989), indicates a degree of plasticity not afforded to strictly nonfeeding lecithotrophs (see also MILLER, 1993 for *Phestilla sibogae*). Further investigation of the possible adaptive significance of egg size variation on survivorship, growth and fitness is evidently expedient.

EGG SIZE VARIATION AND EVOLUTION OF LARVAL TYPES

By definition, nonpelagic lecithotrophy demands greater parental investment in individual eggs than does planktotrophy; therefore egg size tends to covary with larval type. None the less, as HADFIELD & MILLER (1987) showed, the fundamental categories of planktotrophy, pelagic lecithotrophy and nonpelagic lecithotrophy each embrace a range of overlapping egg sizes and there are representatives of each category showing egg sizes within the range 100-170µm. Given that egg size is never fixed for a species or individual, it is inevitable, therefore, that variation within the group as a whole can essentially only be directional — that is for egg size to increase over ecological time. Perhaps this simple statistical feature provides the impetus for selection for increased egg size which must accompany, but not be the sole determinant of, the acquisition of lecithotrophy (KEMPF & TODD, 1989). However, since the individual reproductive adult's resources are finite there will likely be some form of balancing selection to reduce egg size (and maximize numbers), resulting in a continuum of egg sizes and larval types (MCEDWARD, 1997).

As the above observations on larval dispersal in *Adalaria proxima* have shown, the state shift from (presumed ancestral) planktotrophy to (derived) pelagic lecithotrophy may well be facilitated by the genetic consequences of lecithotrophy resulting in genetically isolated (demographically closed) populations; such an evolutionary progression is not, therefore, simply attributable to egg size variation alone. That egg size differs so markedly between populations (Figs. 6, 7) indicates how this can become fixed for populations. But the question remains as to whether or not this variation is adaptive: the indications are that these levels of intraspecific variation in egg size, although striking, are not adaptive and merely reflect drift of differentiated populations (JONES *et al.*, 1996; LAMBERT *et al.*, 2000).

VARIATION IN INDIVIDUAL REPRODUCTIVE BEHAVIOUR

Dioecy does not occur amongst nudibranch species and generally the Order has been categorised as displaying simultaneous hermaphroditism (TODD, 1981; HADFIELD & SWITZER-DUNLAP, 1984). In a wider ecological context there is much current interest in sperm competition and sex allocation in hermaphroditic species (e.g. GREEF & MICHIELS, 1999). In the past, a widely-held perception has been that the differential requirements in provisioning individual sperm and oocytes imply that sperm (and the male sex) could be considered 'cheap'. However features of especial current interest include the conjecture that an increase in sperm competition should occur with increases in multiple mating of individuals — 'first male precedence' *versus* 'last male dominance'. Another is that an elevation in investment in the male sex should result from either or both of sperm digestion and the obligatory reciprocal transfer of sperm. All of these features can lead to an equal investment in the two sexes by internally fertilizing hermaphrodites. Given the ease of rearing and maintaining many nudibranch species in the laboratory, the group would appear to be well-suited model systems for such investigation. Many aspects of reproductive behaviour of nudibranchs are poorly understood, but it is highly likely that reciprocal transfer of sperm is obligatory during copulation and the widespread occurrence of multiple or profligate mating of

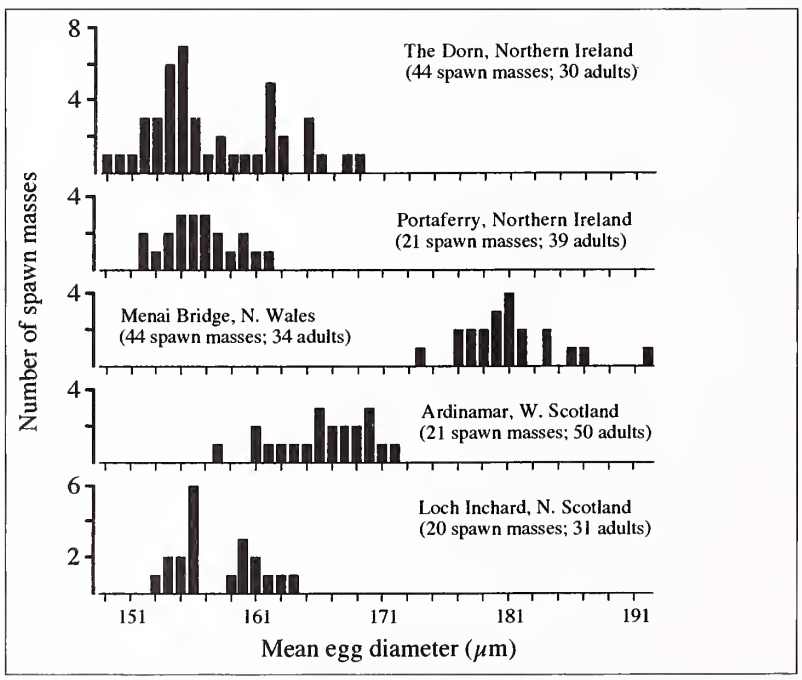

Fig. 6. *Adalaria proxima*. Mean egg diameters (microns) for spawn masses laid by groups of individuals (1993-94 generation) collected from five field sites as prespawning adults (February 1994). The site location details are given by TODD *et al.* (1997a).

individuals between spawnings, and the presence of a gametolytic (sperm digestion) gland, lead to the expectation that sperm competition may be of considerable ecological importance in this group.

Phestilla sibogae illustrates the potential for investigating variation in individual reproductive behaviour amongst this group (TODD *et al.*, 1997). We showed that sperm storage and multiple 'paternity' of an individual's zygotes is common in this species. More important, far from being a simultaneous hermaphrodite, *P. sibogae* is functionally male at an extremely small body size and sperm exchanged (and stored) as a juvenile are disproportionately successful in fertilizing oocytes in fully grown adults (TODD *et al.*, *op. cit.*). As spawning adults, however, individuals do function as simultaneous hermaphrodites. Early juvenile insemination possibly does not occur for all individuals in the field, but it is prevalent in laboratory cultures. Even if at relatively low frequencies in the field, such behaviour is likely to be strongly selected for in this species because of the intensity of fish predation (e.g. GOCHFELD & AEBY, 1997) and the likelihood of the few individuals which survive to an adult size failing to locate an adult mate: large spawning adults are seldom found in the field and copulation between individuals differing markedly in size is presumably unlikely.

For this species at least, therefore, there appears to be a strong selective advantage in fertilizing and being fertilized early — that is, first male/partner precedence. The earliest received sperm are very few in number but disproportionately successful, perhaps as a result of receiving nutritive gain or capacitation advantage over later-received sperm, or even to being less vulnerable to digestion by the gametolytic gland. Whether similar reproductive variability is widespread amongst the Order remains to be ascertained because assessments of genetic non-conformity of offspring and parents have been made for only this one species; but the fact that most nudibranch species typically are rare, or at least of low population densities, and that all are obligate cross-fertilizers are strongly indicative that it ought to be.

SIZE ASSORTATIVE MATING

Size assortative mating is a "positive correlation between the sizes of mates within a population or sample" (ARNQVIST *et al.*, 1996), and assortative mating "sexual reproduction involving the non-random pairing of individuals which are more closely alike than the average (positive) or less alike than the average (negative) in respect of one or more traits" (LINCOLN *et al.*, 1982). In dioecious species showing a positive relation between size and fecundity of females, there is an apparent selective advantage for males to copulate with larger females. However, the time invested in copulating with an individual female, and the amount of sperm that should be transferred renders the situation complex. This is especially pertinent for nudibranchs, amongst which multiple copulation is prevalent and given the foregoing problems associated with sperm dilution. For hermaphrodite species this becomes even more intricate, especially if reciprocal transfer of sperm is obligatory, because individuals can maximize their fitness both as a male and female. For smaller individuals, the advantage in fertilizing (and being fertilized by) a larger individual is clear but the reverse is not. Even for strongly seasonal species, in which all individuals are of closely similar age, marked variation in size at reproduction is apparent. Fig. 8 shows the length frequency distribution for an intertidal population of the barnacle predator *Onchidoris bilamellata*. As expected, the distribution is unimodal but the length range is considerable and body mass of this species increases by a factor of 5 for a doubling of length. The effective breeding population in Fig. 8 will be fewer than the 206 individuals sampled because the smallest dorids probably will fail to produce spawn. The effective population size probably will be yet smaller, because of limited numbers of suitably-sized mates for large and small individuals, unless there is strong positive assortative mating for both smaller and larger individuals.

The potential for nudibranchs as model systems in assessing assortative mating both in the laboratory and field is apparent from such size distribution data alone, but morphological problems probably also are implicated in pair formation in nudibranchs. Opisthobranch reproductive systems are structurally complex, and the manner in which the penes of copulating individuals become interlocked indicates major mechanical difficulties for copulation between individuals of markedly differing size. This variable becomes especially acute when considering how much these animals degrow during their reproductive period (e.g. HAVENHAND & TODD, 1988b). But is it just the body wall that shrinks (= 'deflates'), or do all the body organs degrow allometrically? If nudibranchs are limited in the size range of partners with which they can copulate, does that size range (and hence the number of potential partners) change during the individual's reproductive period? In the absence of assortative mating, do individuals of intermediate size have the greatest range of potential partners available, and do they therefore elevate their fitness over larger counterparts by maximizing their male function? These and related questions have yet to be assessed for nudibranchs.

POECILOGONY

Developmental variability amongst marine invertebrates is perhaps expressed at its most extreme by the condition of poecilogony, and studies of opisthobranchs have provided some controversial examples (HOAGLAND & ROBERTSON, 1988; BOUCHET, 1988; CHIA *et al.*, 1996). Poecilogony can be defined as "intraspecific variation in the duration of ontogenetic stages induced by environmental factors" (LINCOLN *et al.*, 1982), but larval ecologists have utilised the term specifically to categorise those species which produce offspring which are separable according to their larval type. The latter application conforms to the previous definition in being quantitative (the egg-to-juvenile period differing in duration according to larval strategy; see also HAVENHAND, 1993) but it also is qualitative because of the contrasting morphology and ontogeny of the offspring. Poecilogony is seemingly very rare amongst marine invertebrates and essentially confined to polychaetes and opisthobranchs (BOUCHET, 1989; GIBSON, 1995; GIBSON & CHIA, 1995; CHIA *et al.*, 1996), and there are sound theoretical

grounds for supposing that selection should favour one strategy or the other, but not either/or within a species. Many suspected cases of poecilogony — especially those concerning geographically disjunct populations displaying contrasting larval types — have proven to involve cryptic species (HOAGLAND & ROBERTSON, 1988; HIRANO & HIRANO, 1991; CHIA *et al.*, 1996), but it is of interest that amongst opisthobranchs, and ascoglossans and nudibranchs in particular (BOUCHET, 1989), there now are several cases of poecilogony — albeit that these examples are open to differing interpretations (e.g. CARROLL & KEMPF, 1990).

For the small hydroid-grazing aeolid, *Tenellia adspersa* (=*pallida*) (Nordmann), EYSTER (1979) deduced poecilogony (pelagic larvae and capsular metamorphosis) in disjunct and single populations respectively, but the possibility of two sympatric cryptic species cannot be eliminated because single egg masses and individual adults gave rise to only the one larval type. EYSTER (1979) did not culture the pelagic veligers of *T. adspersa* through metamorphosis, but her illustration of the hatched larvae (her Fig. 2A) is indicative of a planktotrophic larva, in that the somatic tissues within the shell and the foot development are minimal and there are apparently no eyes. If truly a case of poecilogony, this therefore would be an example of planktotrophy/lecithotrophy. For apparently the same species, CHESTER (1996) subsequently showed clear developmental plasticity in response to food availability to the individual reproductive adult, but this did not involve planktotrophic larvae; starvation of *T. adspersa* resulted in fewer, smaller eggs, all of which hatched as pelagic lecithotrophic veligers whereas control animals fed *ad libitum* showed 10-15% of offspring undergoing capsular metamorphosis.

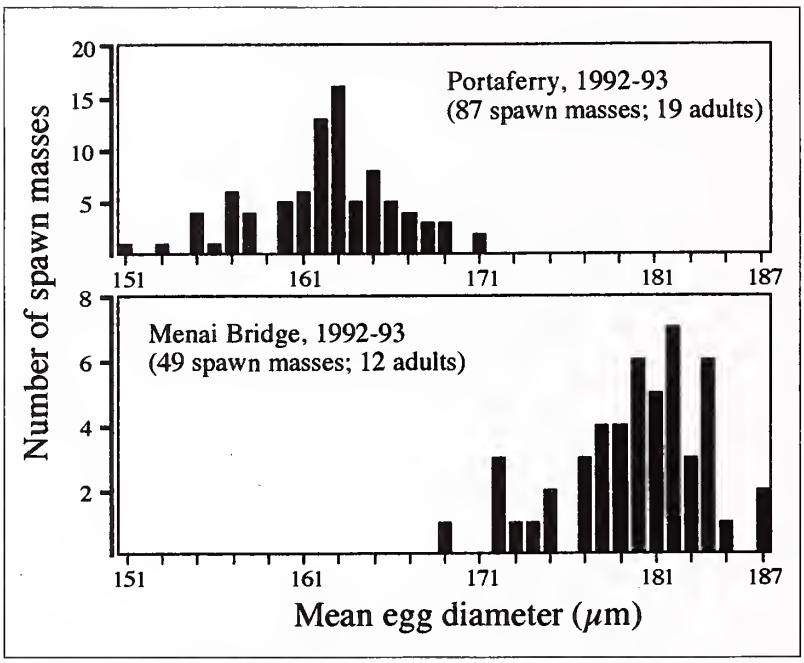

Fig. 7. *Adalaria proxima*. Mean egg diameters (microns) for spawn masses laid by 19 individuals (1992-93 generation) collected from the two field sites as post-metamorphic juveniles (1-2 mm) in August 1992. Individuals were reared to spawning for 9+ months under identical temperature/photoperiod nd feeding conditions. See Fig. 6 and text for details of the between-year comparisons of mean egg sizes for each site.

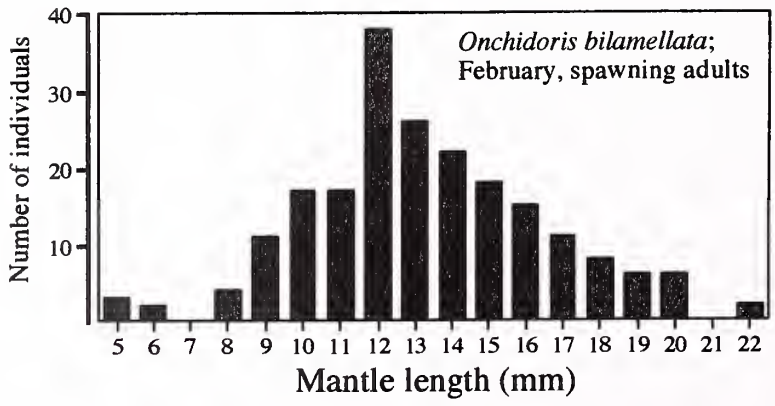

Fig. 8. *Onchidoris bilamellata*. Length frequency histogram for 206 individuals sampled intertidally (Robin Hood's Bay, NE England) at peak spawning (February 1975).

CHESTER (1996) found that capsular metamorphosis not only declined to zero on starvation of adults, but that it could be regained to levels of 32% of larvae produced by adults given access to food again. The need for molecular genetic studies of this species is clear in order to resolve the taxonomic issues: one or more species may or may not be involved, but true peocilogony is apparent.

CARROLL & KEMPF (1990) observed hatching of pelagic lecithotrophic larvae or of (capsular metamorphic) fully-formed benthic juveniles of the anemone predator, *Berghia verrucicornis* Costa, according to whether or not spawn cultures were aerated in culture. Whether this is true poecilogony is open to argument, and of particular relevance here is whether or not encapsulated larvae can acquire and respond to a prey-derived metamorphic cue or if capsular metamorphosis is not cue induced. Although the presence of the prey anemone, *Aiptasia pallida* (Verrill), resulted in significantly higher metamorphosis of larvae, CARROLL & KEMPF (1990) noted that a specific habitat-related cue was not obligatory for metamorphosis to occur. The possibility remains that *B. verrucicornis* merely displays a behavioural variation that leads to non-specifically induced metamorphosis occurring a little earlier or later. Although not a case of poecilogony in the strict sense, this species may present an evolutionary transitional state between pelagic and nonpelagic lecithotrophy as discussed elsewhere (KEMPF & TODD, 1989).

Amongst the opisthobranchs, without doubt the most extreme, and best documented, case of poecilogony is the ascoglossan *Alderia modesta* (Lovén), a specialist grazer of the alga *Vaucheria longicaulis* Hoppaugh. Larvae of *A. modesta* metamorphose in response to waterborne and surface-associated carbohydrates and KRUG (1998) has demonstrated both planktotrophy and pelagic lecithotrophy in the one species, as confirmed by mtDNA sequencing. Most spawn masses developed either as planktotrophic or pelagic lecithotrophic larvae, but a very few (1%) showed the full range of egg sizes and a mixture of planktotrophic and lecithotrophic veligers. This is rather different to the apparent case of poecilogony in the tropical ascoglossan *Elysia cauze* Marcus (CLARK *et al.*, 1979), in which the spawn masses from a single mollusc were of the one developmental type but the incidence of Types 1 (planktotrophic; spring), 2 (pelagic lecithotrophic; summer) and 3 (nonpelagic lecithotrophic; autumn/winter) development varied seasonally. As reviewed by HOAGLAND & ROBERTSON (1988), there are some taxonomic uncertainties in this example; the possibility remains that more than one species was involved and all spawn masses and adults displayed only the one developmental type.

Switching of development of nudibranchs between pelagic lecithotrophy and capsular metamorphosis is conceptually easy to envisage if it were attributable to, say, pleiotropic effects of perhaps only a few genes leading to small temporal shifts in competence and metamorphosis in the absence of a specific inductive cue (e.g. *Berghia verrucicornis*, CARROLL & KEMPF, 1990). A more problematic case, however, is the cephalaspidean *Haminaea callidegenita* Gibson & Chia (GIBSON, 1995; GIBSON & CHIA, 1995), which also has lecithotrophic development, and which may undergo either capsular metamorphosis or release of lecithotrophic larvae, the latter with a potential pelagic life of up to 30 d. The incidence of capsular metamorphosis in *H. callidegenita* shows extreme variation among spawn masses, populations and years; functionally, therefore, poecilogony in this species is much more complex than for *B. verrucicornis* in view of the potential longevity of the pelagic larval stage. Although the percentage of hatching form (benthic juvenile or veliger) of *H. callidegenita* varied 4-100% between years, populations and clutches, all individuals showed variability in this trait. The developmental shift was not attributable either to adult or embryonic culture conditions, but adult food stress did appear important. Food deprived *H. callidegenita* initially produced more swimming larvae than did control females (GIBSON & CHIA, 1995).

Notwithstanding the foregoing, the genetic, cellular and ontogenetic basis of extreme poecilogony, involving the switch between planktotrophy and lecithotrophy, is much harder to envisage because that evolutionary shift demands changes not simply in egg size/embryonic resources (cf. WRAY, 1995). Alterations at the tissue, cell and subcellular levels — especially in relation to food capture/locomotion, feeding, digestion and overall development of the sensory and motor nervous systems (KEMPF & TODD, 1989) — are necessary in the shift from planktotrophy to lecithotrophy. The deployment of extrazygotic yolk within the stroma of the spawn mass is not infrequent amongst ascoglossans and may be a major factor explaining developmental variation across the Opisthobranchia (BOUCHET, 1989). None the less, *A. modesta* undergoing extreme poecilogony in the absence of extrazygotic yolk indicates the possibilities of more examples occurring within the Nudibranchia.

If extreme poecilogony proves to be a more widespread (if not common) strategy than is presently known, such variation presents evolutionary ecologists with a challenging puzzle, and all the more so if it is a feature characteristic of just polychaetes and opisthobranchs (CHIA *et al.*, 1996). Furthermore, as discussed by CHIA *et al.* (1996), reduced salinity appears to be a related factor in many examples. CHESTER (1996) reared *Tenellia adspersa* at a reduced salinity of 20 ppt but did not address the possible influence of salinity variation on developmental type. Notwithstanding such gross environmental effects, the levels of interspecific and intraspecific variation in such fundamental traits as egg size (e.g. Figs 6, 7) and the range of larval types displayed by nudibranchs leads to the tantalizing suggestion of there being a high probability of many more novelties yet to be discovered. But the question remains as to whether or not such variation is truly adaptive.

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The types of marine molluscan species described by Monterosato, in the Museo Civico di Zoologia, Roma. General scope of the work, and part 1: the opisthobranch gastropods

Marco Oliverio & Lionello P. Tringali

Personne n'a connu aussi bien que lui la faune malacologique de la Méditerranée.
(DAUTZENBERG, 1928)

He was an extraordinarily accurate and careful observer, and it was very, very seldom that one could challenge his decision in the discrimination of a species; the smaller the shell, the more exact and reliable was his comprehension of it.
(TOMLIN, 1930)

One needs only glance through any major modern guide to the marine mollusks of the Mediterranean to find the name of Monterosato associated with almost every family of marine shells.
(ABBOTT, 1982)

KEY WORDS: Cephalaspidea; Mediterranean; Monterosato; nomeclature; types; Opisthobranchia; Thecosomata.

ABSTRACT The project for a revision of the types of marine species described by T. Di Maria, known as Monterosato, kept in the Museo Civico di Zoologia, Roma (ZMR) is presented, with the purpose of providing a clear check-list of these types with the best possible iconography. The problems encountered while carrying out the project are reported, together with comments on the problematic history of the Monterosato collection. In this first part, the types of the opisthobranchs have been examined. Monterosato introduced ten available specific names, and an infrasubspecific name, raised to subspecific rank by F. Nordsieck befote 1985, now regarded as belonging to the opisthobranchs. They are: *Acteon candidulus* Monterosato, 1923, *Ringicula conformis* Monterosato, 1877, *Cylichnina crebriculpta* Monterosato, 1884, *Haminoea hydatis* var. *cymoelium* Monterosato, 1923, *Spirialis diversa* Monterosato, 1875, *Coleophysis effusa* Monterosato, 1890, *Philine intricata* Monterosato, 1884, *Utriculus minutissimus* Monterosato, 1878, ex H. Martin MS., *Philine monterosati* Monterosato, 1874, ex Jeffreys MS., *Amphispyra quadrata* Monterosato, 1874, *Philine striatula* Monterosato, 1874, ex Jeffreys MS. Type material of all the species have been found in the Monterosato coll. (ZMR), and is here documented. The authors preliminary discuss the identity of the mentioned specific names.

RIASSUNTO Gli autori presentano il progetto per l'individuazione dei tipi delle specie di molluschi marini descritte dal Monterosato e conservate nella sua collezione, presso il Museo Civico di Zoologia, Roma (ZMR). Gli autori si propongono di giungere ad un elenco completo dei tipi conservati, offrendone anche, per quanto possibile, una buona iconografia. Le difficoltà connesse all'attuazione di tale progetto vengono presentate, commentando anche i problemi storici della collezione Monterosato. Vengono qui indicati i criteri sulla base di quali è considerato come tipico il materiale presente nella collezione. In questa prima parte, sono stati esaminati i tipi degli opistobranchi. Gli autori discutono l'identità e disponibilità dei nomi introdotti dal Marchese, identificandone i tipi. Undici nomi di opistobranchi sono considerati disponibili nel senso dell'ICZN (1999: Art. 12): *Acteon candidulus* Monterosato, 1923; *Ringicula conformis* Monterosato, 1877; *Amphispyra quadrata* Monterosato, 1874; *Cylichnina crebriculpta* Monterosato, 1884; *Coleophysis effusa* Monterosato, 1890; *Utriculus minutissimus* Monterosato, 1878, ex H. Martin MS.; *Haminoea hydatis* var. "*cymoelium*" Monterosato, 1923; *Philine intricata* Monterosato, 1884; *Philine monterosati* Monterosato, 1874, ex Jeffreys MS.; *Philine striatula* Monterosato, 1874, ex Jeffreys MS.; *Spirialis diversa* Monterosato, 1875. *Acteon candidulus* – di cui restano soltanto due sintipi – sembra basato su conchiglie scolorite e erose di *Acteon tornatilis* (Linné, 1758) (cft. SMRIGLIO & MARIOTTINI, 1996). Patecchi sintipi di *Ringicula conformis* sono conservati al Museo. Questa specie è certamente distinta da *Ringicula auriculata* (Menàrd de la Groye, 1811), sia per la presenza di un dente parietale in più, che per la protoconca dal nucleo meno sporgente e con diametro inferiore – la presenza di una protoconca I e di una protoconca II indica che *conformis* avrebbe sviluppo planctotrofico. *Amphispyra quadrata* – di cui resta poco materiale in mediocre stato di conservazione – sembra essere un sinonimo di *Colpodaspis pusilla* M. Sars, 1870. «*Diaphana quadrata* (Monterosato, 1874)» *sensu* NORDSIECK (1972) è specie diversa, forse non descritta (cft. OLIVERIO, 2000). Tutto il materiale tipico di *Cylichnina crebriculpta* nel Museo, identificabile come tale, è costituito da due conchiglie di Palermo. La distinzione delle specie a spira immersa del genere *Retusa* T. Brown, 1827 – spesso attribuite al (sotto)genere *Cylichnina* Montetosato, 1884 - appare ardua, tuttavia *C. crebriculpta* potrebbe rientrare nella variabilità di *Retusa strigella* (Lovén, 1846) – l'identità di *Bulla umbilicata* Montagu, 1803, data per evidente in letteratura, è, invece, tutt'altro che chiara e perciò è qui adottato il nome di Lovén. Il materiale tipico di *Coleophysis effusa* – 5 conchiglie – è stato identificato mediante un complesso di indizi, non essendo stato cartellinato come tale per mano di Monterosato stesso. La specie sembrerebbe essere una forma a debole scultura assiale di *Retusa truncatula* (Bruguiére, 1792), forse prossima alla forma "*pellucida*" T. Brown, 1827. *Utriculus minutissimus* è rappresentato da numerosi sintipi nella collezione. Erroneamente collocata da vari autori in *Pyrunculus* Pilsbry, 1895, è, in tealtà, una vera *Retusa*, come mostrano la conchiglia e le piastre gastriche; è distinta da *R. obtusa* (Montagu, 1803), di cui a volte, soprattutto dagli Autori nordici, è stata considerata forma immiserita delle acque mediterranee. Il nome *Haminoea hydatis* var. *cymoelium* è stato elevato al rango di sottospecie prima del 1985 (NORDSIECK, 1972) e, petciò, è nome disponibile. Al Museo se ne conserva l'olotipo, che, tuttavia, appare determinabile come una *Haminoea hydatis* (Linné, 1758) scolorita. In linea con VAN DER LINDEN (1994), gli autori considerano che il nome *Philine intricata* sia stato validamente introdotto da MONTEROSATO (1884), piuttosto che da MONTEROSATO. (1875), che non contiene nessuna caratteristica descrittiva della specie. Il materiale relativo a *Philine intricata* è abbastanza ricco, laddove sono pochi i sintipi di *Philine monterosati*, di cui sono qui raffigurate anche i denti radulari e le piastre gasttiche. *Philine striatula* è una vera *Philine* Ascanius, 1772, una specie valida per la quale è da adoperare questo nome. Oltre che presente in Mediterraneo e lungo le coste europee occidentali, vive anche in Africa occidentale. L'unico Thecosomata Blainville, 1824, descritto da Monterosato è *Spirialis diversa*, specie valida, già largamente discussa in letteratura, di cui sono stati rinvenuti nella collezione pochi sintipi in cattivo stato, ma ben riconoscibili. I nomi *Tornatina detruncata*, *Bulla globosa*, *Philine* [o *Laona*] *membranacea*, *Cylichna obesiuscula*, *Retusa (Coleophysis) pyriformis* [o *piriformis*], *Bulla subquadrata*, attribuiti da alcuni autori a Monterosato, non furono mai introdotti dal Machese in modo valido; nella maggior parte dei casi, anzi, non sono neppure citati nei suoi scritti.

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GENERAL SCOPE OF THE WORK

There is no doubt that Tommaso Di Maria, nobleman of the barons of Allery, and marquis of Monterosato (Palermo, June 27st, 1841 - ibidem, March 1st, 1927) was among the leading European malacologists in the second half of the nineteenth century. Along with John Gwyn Jeffreys, Wilhelm Kobelt, Philippe Dautzenberg, Georg Ossian Sars, he produced outstanding works on the systematics and the biogeography of the Northeast Atlantic molluscs, mainly marine, Fossil and Recent. The excessive inclination for splitting affecting his latest works – admitted, even critically, by the Marquis himself (see e.g. MONTEROSATO, 1896: 20 \1104\; 1906: 130 \1162\) - does not compromise such a wide and significant malacological corpus. The major outcomes within his works are certainly his highly valuable check-lists of Mediterranean seashells (MONTEROSATO, 1872; 1875; 1878a; 1884), although several minor notes also contain significant contributions. A large number of generic and specific names were introduced in his works, many of which are currently employed. He introduced more than five hundred species-level names. Some 70% of these are available, but further specific names, originally introduced as variety names, were later on raised to (sub)specific rank by other authors and thus also made available.

The usually concise, even telegraphic descriptions written by Monterosato are in several cases exceptionally keen, fully displaying his skill to outline the shell morphology of a species by means of few incisive words, yet frequently they may leave some doubts, fitting more than one entity likewise. Therefore the reference to the type material is needed to define the identity of the most enigmatic specific names coined by the Marquis. However, this procedure has been at all problematic in the past. The Monterosato collection – «d'une richesse incomparable» in DAUTZENBERG's (1928) words, being among the most imposing historical collection of Mediterranean seashells and Italian continental shells – is kept in the Museo Civico di Zoologia di Roma [= Township Zoological Museum of Rome" (ZMR)] since about 60 years, and it has been unavailable for study since many and many years with sporadic exceptions only.

The authors have been asked by the Scientific Staff of the ZMR to start a critical reordering of the type material of Monterosato's marine species in the ZMR. We started to work on that material in the summer 1997, meeting some hard problems of which the worst was the disorder affecting the collection, a fatal consequence of its troubled history (see e.g., SETTEPASSI, 1985; PIANI, 1982; 1984). At the beginning of his eighties Monterosato promised the collection to a fellow-citizen and collector, the commendator Vito Beltrani in order to ease his difficult economic situation. It seems that the agreement with Beltrani allowed the Marquis to keep for study the collection until the age of eighty-five. Anyway it was definitively lost by Monterosato a year before his death, Beltrani having taken legal proceedings to obtain it. In 1941 a grandson of Beltrani sold the collection to the Zoological Garden of Rome - which included the ZMR up to few years ago - and afterwards it was transferred to the ZMR, where the lots were filed by a Curator of the Museum in the late 1940s or, more probably, in the firsts 1950s.

It is difficult to assess how much the collection was altered by Monterosato himself during his latest years, and by Beltrani. It is well-known that, before the arrival in Rome, important material had already been moved elsewhere. For instance, a good deal of important material is presently stored in the Coen collection at the Hebrew University (Jerusalem) (cf. PIANI, 1984). Furthermore, Monterosato exchanged material with many malacologists around the world, as it is witnessed by the large amount of Monterosato's lots presently in several public collections (USNM Washington, NHML London, MNHN Paris etc.). We have noticed that the labels of many lots were never updated by the Marquis – possibly due to lack of time; see below, the case of *Coleophysis effusa* Monterosato, 1890, and its type material - a fact that obviously increases the difficulty to identify the types. During more than fifty years of permanence in the ZMR, the Monterosato collection was never submitted to any systematic long-term study, until the present project, nor to periodical operations for conservation. Only two Curators had been in charge at the Malacological Section of the ZMR in the last thirty years. The former one, the late Francesco Settepassi, was a very appreciable person, and an amateur malacologist with true passion and good aims. It is to remember that the Monterosato collection came in the ZMR also thanks to Settepassi's advice (cf. SETTEPASSI, 1985). However, it is evident that during his period of activity at the ZMR, ended by his death in 1981, much material was shifted in a chaotic way from the Monterosato collection to other collections in the Malacological Section of the ZMR, while it is likely that some other lots were definitely lost. Beyond all doubts, the "deepest impact" on the Monterosato collection during this period was due to the Malacological Exhibit of Palazzo Braschi in Rome (October 1976), prepared by a team of enthusiastic and willing collectors. Many shells from the Monterosato collection, including syntypes of species by Monterosato, Brugnone, Tiberi, Jeffreys, Brusina, Crosse, Granata-Grillo, Pallary, and others (cf. ANONYMOUS, 1976), were employed, with very little care indeed for both the material (fixed by means of generous quantities of glue on boards, or, if rejected in the final selection, left out of the Monterosato coll., in total disorder) and the original labels, which were lost in part, the remaining ones being often hard or impossible to associate with the lots now. Frequently, the material from the Monterosato collection is mixed with samples from other sources (F. Settepassi collection ZMR, Roman private collections) without any indication useful to identify it.

After Settepassi's death, Dr. Flavia Gravina, a biologist, yet not a malacologist, worked for few years at the ZMR, appointed at the Malacological Section. Since the 1980s up to the beginning of the 1990s the ZMR benefited also the contribution of the late Mrs. Angelina Gaglini, an amateur, yet experienced malacologist, who, gleaning in the Monterosato collection, published some reports (e.g. GAGLINI, 1987; 1991; 1992) until her premature decease. Alongside these papers, a few further occasional notes have been published in the last twenty years being based on the material of the Monterosato collection, mostly on the Italian journals *Notiziario C.I.S.Ma.* and *Bollettino Malacologico*.

Basing on our preliminary survey, the general conditions of the Monterosato collection leaves much to desire. Many lots are out of place, a fact that makes rather long and difficult to find the mater-

ial. Furthermore, there is a serious problem of conservation to solve: as frequent in nineteenth century collections, most old glass tubes are corked, with damp deposits inside.This preludes the dangerous formation of butyrate crystals, which may radically alter or even destroy the preserved shells. Unfortunately we have noticed that the butyrate crystals are already damaging some material. PIERSANTI (1942: 252), who was in charge of estimating the Monterosato-Beltrani collection for the purchase by the Direction of the Zoological Garden of Rome, valued at about three millions the number of specimens. This approximate estimate gives a clear indication of the richness of the collection, and the difficulties of a radical conservative intervention. On the other hand the Monterosato collection represents an Aladdin's cave for Mediterranean malacology, containing beside the myriad of shells collected by Monterosato himself, also the collections of Adami, of the abbot Brugnone (including those of Benoit, Libassi, and partly of Calcara), and of Tiberi (the marine material only), as well as much material, including also syntypes, received from many nineteenth century malacologists and collectors: de Folin, Granata-Grillo, Pallary, de Boury, Dautzenberg, Aradas, De Gregorio, Jeffreys, Hanley, A. Issel, P. Fischer, Paulucci, Del Prete, J.T. Marshall, Nobre, Coppi, McAndrew, Weinkauff, Hidalgo, Chaster, Morlet, H. Martin, von Maltzan, Pantanelli, Crosse, R.B. Watson, Petit de la Saussaye, Brusina, Praus Franceschini, Kobelt, Sulliotti, Coen, Jordan, Tomlin, Locard, Terquem, Sacco, Westerlund, Milaschewich, G. Seguenza, and many others. Moreover, Monterosato also obtained from his correspondents material from older authors (e.g. Risso and Scacchi); finally, some types of species described by malacologists of our days were selected among the shells of this monumental collection. Therefore it goes without saying that the full safeguard and reordering of such an outstanding collection is both a scientific and historical duty.

Our project is to single out all Monterosato's marine molluscan types in the ZMR, together with reordering the material and publishing the results of the survey with the best possible iconography. The present contribution is the first step in this work - see below for further details. The level of critical analysis of the material will depend on our experience on the relevant group. Some years ago the Pyramidelloidea of Monterosato were studied by Italo Nofroni (Rome), who worked also on the type material in the ZMR: the results of his survey will be published elsewhere.

As general criteria in the identification of the type material we have adopted the following: (1) all the material explicitly marked as type material by Monterosato himself is obviously typical; (2) all the material from localities quoted in the work where a species was described, or in previous works by Monterosato, is typical if there are no clues suggesting its later collecting – e.g. being dated as later than the description – or its origin from a different correspondent than those quoted in the works; (3) all the material labelled as collected before the publication date of the description is regarded as type material; (4) all the lots indicating the name of the sender, yet not the locality and/or dating, if he is quoted with the description or in previous works is regarded as type material; (5) all the material in lots with doubtful or no indication on the provenance, the sender and the dating, is regarded as not typical; however (6) in very special cases of species lacking further type material, we have regarded as possible types also the material from lots without - or with doubtful - locality data, sender and date; (7) in some further cases, very problematic, we have considered type material even lots without a clear identification by hand of Monterosato, yet identifiable by further details – date, provenance, etc. – as the specimens Monterosato had in his hands describing the species. Peculiar cases will be discussed under their specific remarks.

The pages from Monterosato's works are here quoted by referring to the page numbers of the original works, and, between inverted slashes (e.g.: \138\), to those of the *Opera omnia*, namely the complete malacological works (MONTEROSATO, 1869-1923) collected and edited by Riccardo Giannuzzi Savelli, with the help of Piero Piani, published by the Società Italiana di Malacologia from 1982 to 1989.

DISCLAIMER

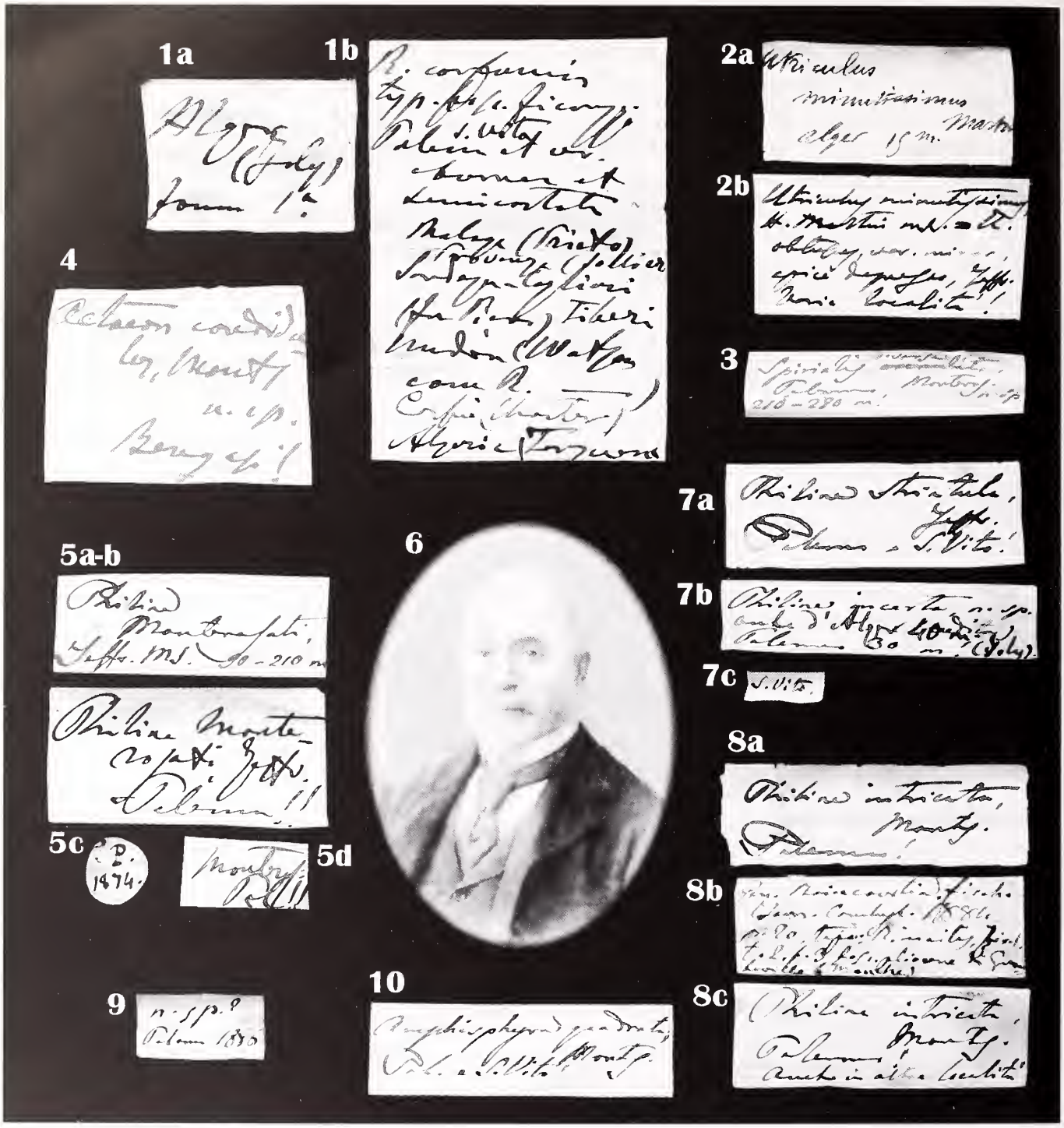
In some cases we will report unpublished names, often found in the original labels. We do not intend by these citations to introduce new names. They are only reported to facilitate tracking of the material or to elucidate the history of nomina nuda.

MONTEROSATO'S OPISTHOBRANCH TYPES

Monterosato introduced ten available specific names, now regarded as belonging to the opisthobranchs. In addition, an infrasubspecific name was raised to subspecific rank by a later author before 1985, becoming an available (sub)specific name according to the ICZN (1999: Art. 45.6). Thus the total is of eleven specific names:

- *Acteon candidulus* Monterosato, 1923
- *Ringicula conformis* Monterosato, 1877
- *Cylichnina crebrisculpta* Monterosato, 1884
- *Haminoea hydatis* var. *cymoelium* Monterosato, 1923
- *Spirialis diversa* Monterosato, 1875
- *Coleophysis effusa* Monterosato, 1890
- *Philine intricata* Monterosato, 1884
- *Utriculus minutissimus* Monterosato, 1878, ex H. Martin MS.
- *Philine monterosati* Monterosato, 1874, ex Jeffreys MS.
- *Amphispyra quadrata* Monterosato, 1874
- *Philine striatula* Monterosato, 1874, ex Jeffreys MS.

Eight species belong to the Cephalaspidea P. Fischer, 1883 [= Bullomorpha Pelseneer, 1906]; two others, traditionally regarded as cephalaspidean gastropods, are now in a problematic position, belonging to the Acteonidae Orbigny, 1835, and the Ringiculidae Philippi, 1853, respectively, thus awaiting for a better defined systematic position (see MIKKELSEN, 1996: 416); finally, there is a single specific name of the Thecosomata Blainville, 1824. Considering the large amount of new specific names in Monterosato's works, the opisthobranch names introduced by the Marquis are rather few indeed. Yet, Monterosato was here more careful than elsewhere, publishing very few nomina nuda (there are also few unpublished nomina in schedis in the Monterosato collection); thus, most opisthobranch names are available having been introduced with a description or an indication (ICZN, 1999: Art. 12).



Figs. 1-10. Original labels of the type material, and a photo of the Marquis – **Figs.** 1a-b: *Ringicula conformis*, «Algiers (Joly) forma 1ª». **Figs.** 2a-b: *Utriculus minutissimus* – Fig. 2a: label in the lot from Algiers, 15 m; Fig. 2b: label on the bottom of the box 16015. **Fig.** 3: *Spirialis diversa* **Fig.** 4: *Acteon candidulus*. **Figs.** 5a-d: *Philine monterosati* (Fig. 5c: cork of the tube with the syntype found within the material of the Exibit). **Fig.** 6: Tommaso Di Maria, dei Baroni di Allery, Marchese di Monterosato. **Fig.** 7a-c: *Philine striatula* (note that on the label in Fig. 7b the species is named «*Philine incerta* n. sp.», a manuscript name; Fig. 7b is the label on the bottom of the box 16322). **Figs.** 8a-c: *Philine intricata*. **Fig.** 9: *Coleophysis effusa*. **Fig.** 10: *Amphispyra quadrata*. – All but one labels by hand of Monterosato; the label in Fig. 2a by hand of Joly.

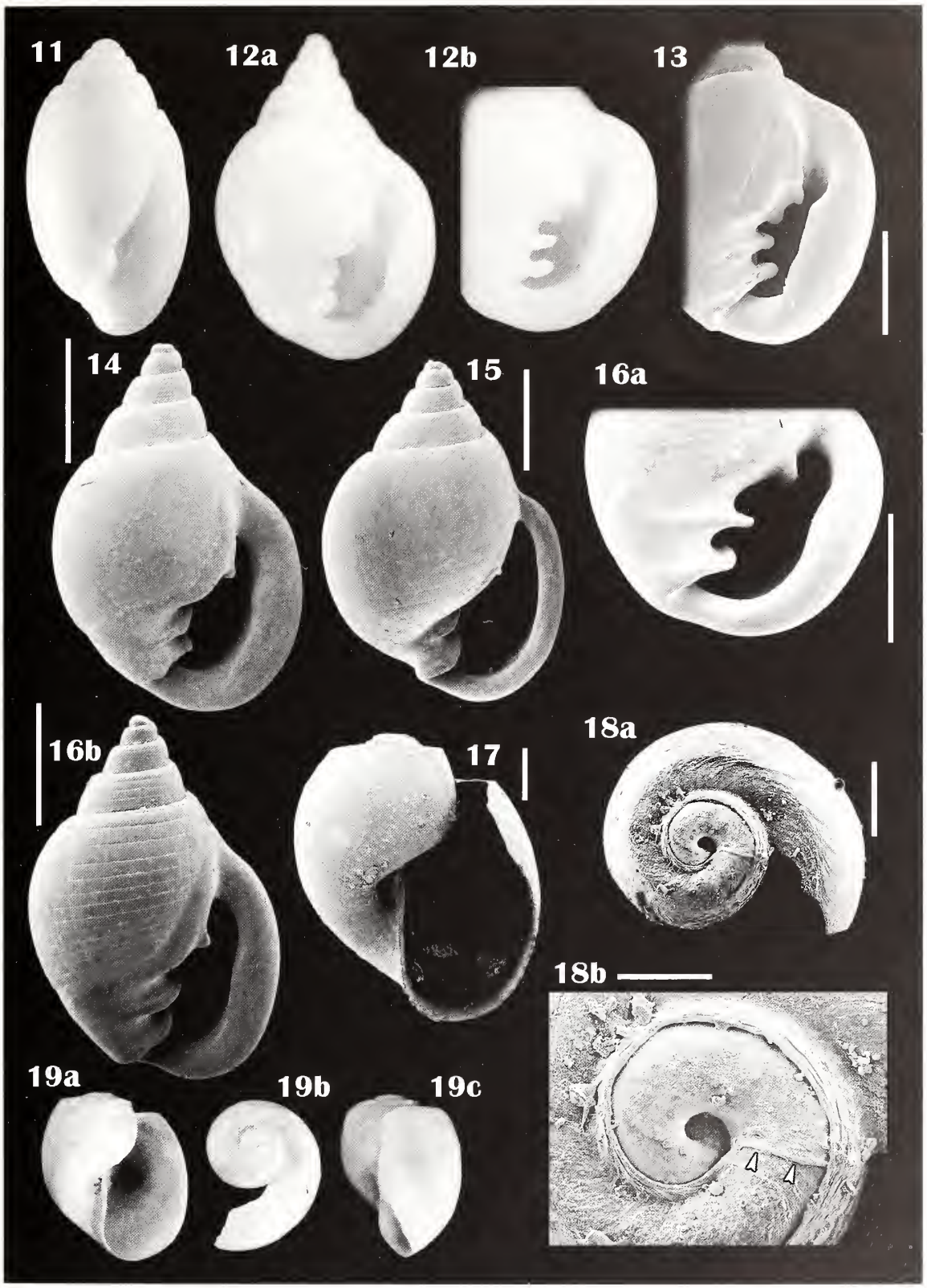


Fig. 11: *Acteon tornatilis* (Linné), syntype of *Acteon candidulus*, Bengasi (Libya) (h: 8.0 mm). **Figs. 12-15:** *Ringicula conformis* – Figs. 12a-b: syntype, labelled «Algiers (Joly) forma 1ª», Algiers (h: 2.9 mm) (note the couple of parietal teeth); Fig. 13: West Sahara, between 24°-25° N lat, 40-60 m, from stomach contents of flatfish (fam. Pleuronectidae) (note the couple of parietal teeth); Fig. 14: syntype, Algiers (labelled «Algiers (Joly) forma 1ª»); Fig. 15: syntype, Algiers (labelled as «Algiers (Joly) forma 2ª»). **Figs. 16a-b:** *Ringicula auriculata* (Ménard de la Groye), Algiers (P. Joly legit, Monterosato coll.) (note the single parietal tooth). **Fig. 17-19:** *Colpodaspis pusilla* (M. Sars), syntypes of *Amphispyra quadrata* - Fig. 17: between Cape San Vito and Palermo; Figs. 18a-b: Cape San Vito; Figs. 19a-c: between Cape San Vito and Palermo (h: 1.1 mm). **Scale bars:** 1.0 mm (13, 14, 15, 16b); 200 µm (17, 18a); 100 µm (18b).

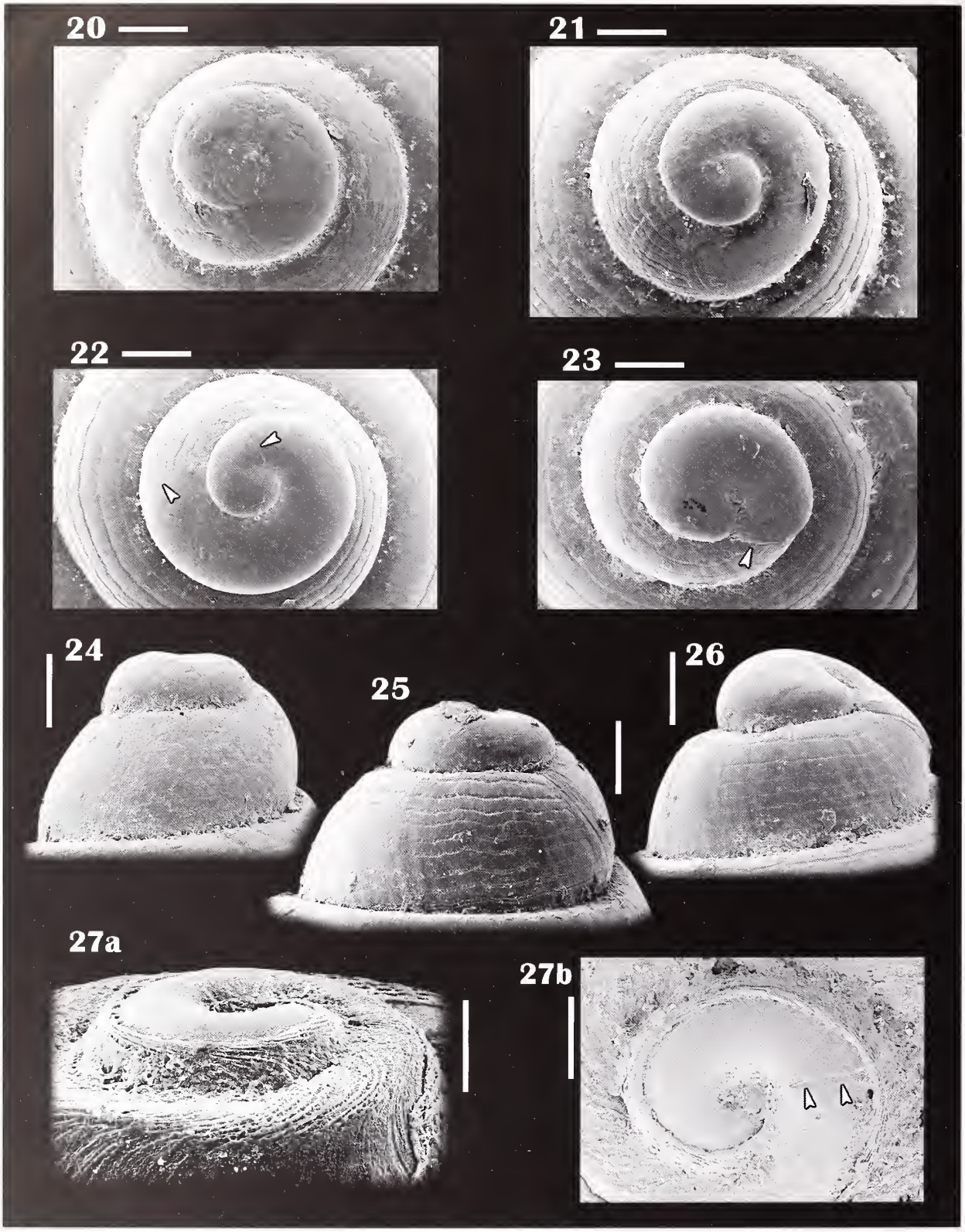


Fig. 20-22: *Ringicula conformis*, protoconch in apical view - Fig. 20: paralectotype, Algiers (labelled as «Algiers (Joly) forma 1ª»); Fig. 21: paralectotype, Algiers (labelled as «Algiers (Joly) forma 2ª»); Fig. 22: West Sahara (data as Fig. 13) (arrows point to the boundaries between protoconch 1-protoconch 2, and between protoconch–teleoconch) (F. Gubbioli legit, LPT coll.). **Fig. 23:** *Ringicula auriculata* (Ménard de la Groye), Algiers (Monterosato coll.) (arrow points to the protoconch–teleoconch boundary). **Figs. 24-25:** *Ringicula conformis*, protoconch in lateral view - Fig. 24: paralectotype, Algiers (labelled as «forma 1»); Fig. 25: paralectotype, Algiers (labelled as «forma 2»). **Fig. 26:** *Ringicula auriculata* (Ménard de la Groye), Algiers, protoconch in lateral view. **Figs. 27a-b:** *Colpodaspis pusilla*, protoconch, Persgrund, Koster Area, (Western Sweden), sand-clay, 20-40 m (C. Schander legit, LPT coll.) (arrows on Fig. 27b point to protoconch–teleoconch boundary). Scale bars: 100 µm.

Like for many other groups of seashells, Monterosato fully displayed also on Mediterranean opisthobranchs his wide and deep knowledge. Most of the described taxa are valid species; a good part of them are the valid names to use (ICZN, 1999: Art. 23).

Generally speaking, the opistobranch lots in the Monterosato collection are in much better condition than other groups, arguably because opisthobranchs have not elicited a great interest by the collectors and malacologists who could access to the collection in the past. Despite some syntypes being obviously lost, we have been able to identify type material for all the opisthobranch taxa introduced by Monterosato. In some cases, this was by means of a complex of circumstantial, yet convincing evidences. The quoted type material is accompanied by remarks on each species. Some names of varieties described by Monterosato have never obtained the status of available names, having not been used at a (sub)specific rank by any workers before 1985. Being now unavailable names, they have been excluded from the list.

Abbreviations and acronyms

coll.: collection;
frg./frgs.: shell fragment(s);
LPT: Lionello Paolo Tringali, Rome;
MO: Marco Oliverio, Rome;
sh./shs.: specimen(s) collected without soft parts;
spm./spms.: specimen(s) collected with soft parts;
ZMR: Township Zoological Museum, Rome, ("Museo Civico di Zoologia, Roma").

The notation «!» in the original labels and in the works by Monterosato stands for "personally checked".

Notice also that «Ficarazzi», frequently quoted in the labels and works by Monterosato, is the locality in the district of Palermo, not the homonym near Catania (both in Sicily).

SYSTEMATIC PART

Ordo CEPHALASPIDEA P. Fischer, 1883 [s.l.]
Familia ACTAEONIDAE Orbigny, 1835

***candidulus*, *Acteon* Monterosato, 1923**

First valid introduction - Monterosato (1923: 12 \1317\; unnumbered pl. \1319\, fig.17), by means of a description and a figure.

Type material - Two sh. from Bengasi (Libya), unrecorded depth, (C. Crema legit) from the box 16053 (original label: «*Actaeon candidulus*, Monts. n. sp. Bengasi!», Fig. 4) (Fig. 11).

Remarks - The locality on the label fits the locality quoted for the shell figured by Monterosato (1923). Despite that photo published with the original description is of poor quality, it may be reasonably argued that the shell is the same here figured. It is a rather worn and faded shell. The unfigured syntype is even in worse conditions, being also broken. Monterosato (1923) wrote to had obtained «Tre soli esemplari, dei quali uno intero» (viz. "Only three specimens, a single one of which being complete"). However Smriglio & Mariottini (1996: 189, 191; 190, figs. 17a-18b) found and figured only two shells from the Monterosato collection, box 16053. The files listing the material arrived to the ZMR remark that the box 16053 contained two shs of *A. candidulus*. Therefore the third shell was lost before the collection arrived at the ZMR. As already noticed by Smriglio & Mariottini (1996) the syntypes seem to be worn shells of *Acteon tornatilis* (Linné, 1758), thus making *A. candidulus* a junior synonym of the latter. Although the variable shell morphology of *Acteon tornatilis* could possibly conceal a complex of species, we think that the conclusion by Smriglio & Mariottini (1996) must be accepted.

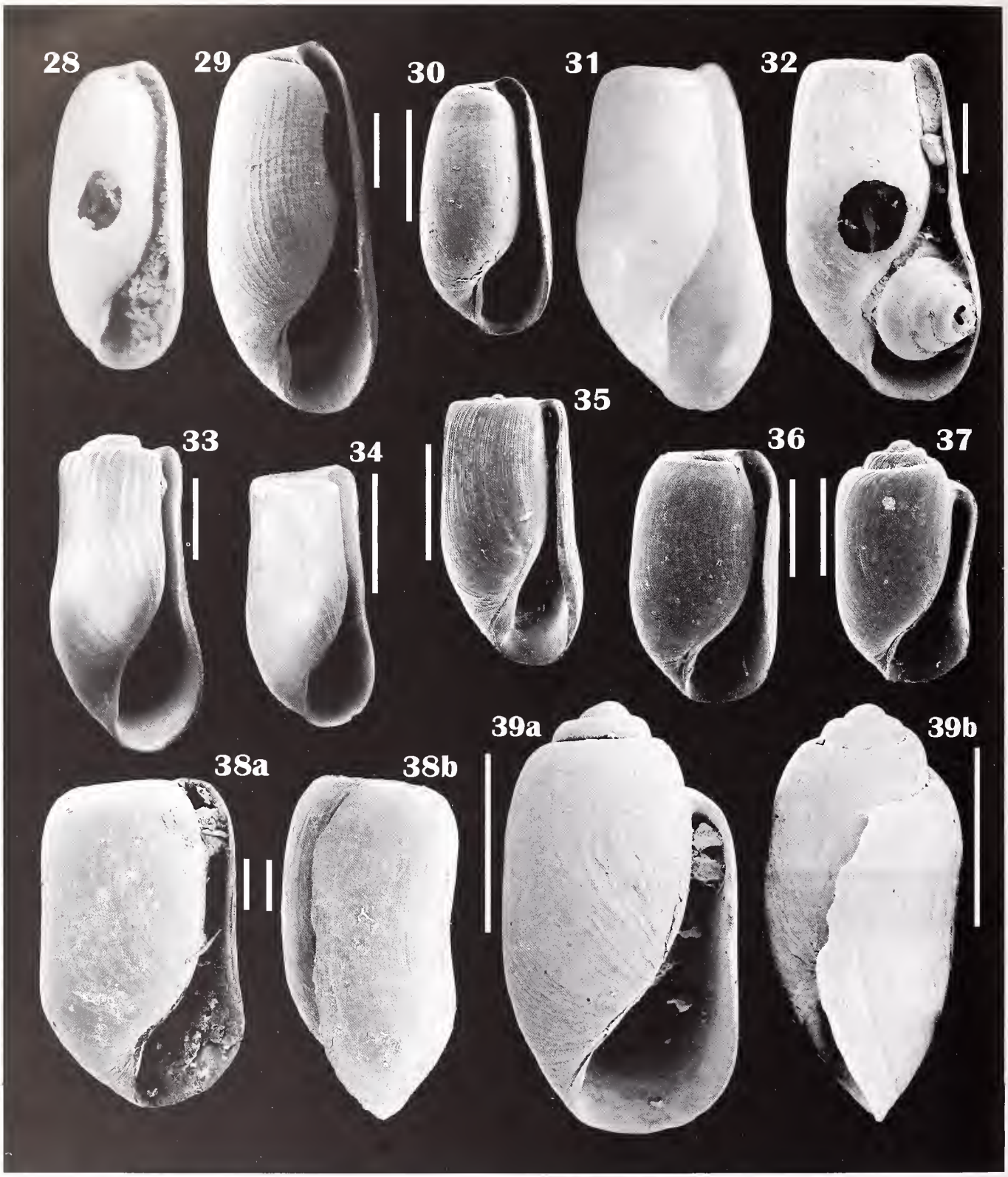
Familia RINGICULIDAE Philippi, 1853

***conformis, Ringicula* Monterosato, 1877**

First valid introduction - Monterosato (1877: 44 \314\; pl. II \321\, figs. 4) by means of a description and two figures.

Type material - 5 shs., Algiers (Algeria), unercorded depth, (P. Joly legit), (original label: «Algiers (Joly) forma 1ª») (Figs. 12a-b, 14, 20, 24); 2 shs., Algiers, labelled as «Algiers (Joly) forma 2ª», (P. Joly legit) (Figs. 15, 21, 25); 7 shs. and several fragments, Palermo [labelled as «*R. conformis* v. *eburnea* M. Palermo!»] - all type material from the box 16280, which bears on the bottom the label: «*R. conformis* typ. foss. Ficarazzi Palermo S. Vito et var. *eburnea* et *semicostata* Malaga (Prieto) Provenza (Sollier) Sardegna Cagliari (Fr [illegible]) Tiberi Madera (Watson come *R.* _) Corfù (Chaster) Algeria, Toscana».

Remarks - The material at the base of the work in which *Ringicula conformis* was described, was collected by Joly in the harbour of Algiers (Monterosato, 1877: 25 \295\). However, describing the species, Monterosato (1877: 44 \314\) remarked that it was obtained from several localities in the Mediterranean, inhabiting also the Atlantic waters. We consider likely that Monterosato had already found material of *R. conformis* from Palermo - his main area of research - when he quoted *R. conformis* as variety of *Ringicula auriculata* (Menàrd de la Groye, 1811) two years before (Monterosato, 1875: 45 \271\), so that the sample from Palermo is here regarded as type material. We consider that many shells labelled as *R. conformis* in the boxes 16280 and 16296 cannot be pointed out as syntypes - box 16280: 1 shell, harbour of Cagliari (Sardinia), with a label not by hand of Monterosato; 2 shells, coralligenous bottom, likely from Palermo, with a label not by Monterosato; box 16296: 12 Fossil shells, Monreale (Palermo); 3 Recent shells, with a label problematic to read and not in Monterosato's handwriting; 2 shells, Capri Is., (*leg.*: Chaster, 1896); 2 Fossil shells, Ficarazzi (Sicily) labelled as var. "*pusilla*" Brugnone (a manuscript name), by Brugnone himself; 4 juv. shells, Ficarazzi, from Brugnone coll.; 6 Fossil shells, Mt. Pellegrino (Palermo), labelled by Monterosato; a tube with 7 Fossil shells labelled «*R. conformis* tipo di Ficarazzi fossile» ("*R. conformis* Fossil type from Ficarazzi"); 109 Fossil shells (2 shells are *R. leptocheila*-group), Ficarazzi, labelled by Brugnone; 2 Fossil shells, labelled «[illegi-



Figs. 27-28: *"Cylichnina" crebriculpta*, syntypes, Palermo (Fig. 28, h.: 2.4 mm). **Fig. 30:** *Retusa strigella* (Lovén), Lilleskär, Koster area, (Western Sweden), mud 30 m. **Figs. 31-34:** *Retusa truncatula* (Bruguière) [s.l.] - Fig. 31-32: syntypes of *Coleophysis effusa*, Palermo (h.: 2.7 mm) (note the shell of *Limacina retroversa* inside the aperture, on Fig. 32); Fig. 33: form with protruding spire, Djerba Is. (Tunisia), unrecorded depth (LPT coll.); Fig. 34: Stn. AKD.92-No. 22, Kash (Turkey), bioclastic sand sample 34 m. **Fig. 35:** *Retusa leptoeneilema* (Brusina), Umag, Dalmazia (Croatia), beached (D. Di Massa legit, LPT coll.). **Figs. 36-38:** *Retusa minutissima* - Figs. 36-37: shells with sunken or protruding spire, Valencia (Southeast Spain), unrecorded depth (Monterosato coll.); Figs. 38a-b: syntype of *Utriculus minutissimus*, Gulf of Fos (South France) (H. Martin legit). **Figs. 39a-b:** *Retusa obtusa* (Montagu), the form probably corresponding to *Bulla pertenuis* Mighels, 1843, Killala Bay (Donegal Bay, Northwest Eire), beached (R. Vallasciani legit, LPT coll.). **Scale bars:** 1.0 mm (30, 33, 34, 35, 39a-b); 500 µm (29, 32, 36, 37); 200 µm (38a-b).

ble] Corsari» [probably Aci Corsari (Sicily)]; 7 shells, labelled «Jean e Luz» (= St. Jean de Luz). A further box (16202) contains material from Algiers (P. Joly legit) and Palermo, labelled by Monterosato as *Ringiculella* species similar to *R. conformis*. The latter is a variable species, and the mentioned material turns out to be *Ringicula conformis* indeed, a form with more evident spiral lines, particularly on the spire. Taking note of the label, however, the shells in the box 16202 are not regarded as type material.

Monterosato obtained from Joly also Algerian material of *Ringicula auriculata* (cf. MONTEROSATO, 1877), still kept in the Monterosato collection, box 16307 or 16308 – there are two numbers in the box - (Figs. 16a-b, 23, 26). Compared with *R. conformis* from the same locality it is evident that they are two distinct species. Along with the differential traits already remarked in literature (CICCONE & SAVONA, 1982: 26) - the second parietal tooth on *R. conformis* (Figs. 12b, 13), lacking on *R. auriculata* (Fig. 16a), and its less marked, more randomly set spiral lines - it is to notice the different apical morphology. The protoconch of *R. conformis* (Figs.20-22, 24, 25), suggesting a planktotrophic larval development, shows a nucleus with a smaller diameter, less swollen and protruding in lateral view than on *R. auriculata* (Figs. 23, 26), which is possibly non-planktotrophic. Monterosato distinguished in schedis two forms from Algiers, as form 1 and form 2, the latter being slightly more swollen and thin. However it is compelling to judge both forms as one single variable species.

Familia DIAPHANIDAE Odhner, 1914

***quadrata*, *Amphispyra* Monterosato, 1874**

First valid introduction - MONTEROSATO (1874: 280 \206\) by means of a description.

Type material - Eleven shs., more or less damaged, from Palermo or Cape San Vito (West Sicily), unrecorded depth - the original sample was mixed in a single tube (original label: «*Amphispyra quadrata*, Monts., Pal. e S.Vito»)- from box 16129; 1 sh. and 1 frg. from Cape San Vito, from a box with no number. (Figs. 17, 18a-b, 19a-c)

Remarks - MONTEROSATO (1874) quoted a single specimen from Cape San Vito, and an unspecified number of specimens from Palermo. However, the material being mixed in the tube from box 16129, it is impossible to decide which are the shells from San Vito and which are from Palermo, though, taking account of Monterosato's words, it is likely that he had more shells from Palermo. Anyway Palermo and Cape San Vito are quite close localities on the Sicilian Northwest coast, so that it is trivial whether the material comes from one or the other . On a label placed on the bottom of box 16129 Monterosato wrote: «[...] Anche di Taranto». However no tubes with material labelled as coming from Taranto (Southeast Italy) are in the Monterosato coll.

The type material of *Amphispyra quadrata* seems to confirm LEMCHE's (1948: 40)view about the synonymy of Monterosato's taxon with the North Atlantic *Colpodaspis pusilla* M. Sars, 1870. The comparison of the type material and 2 shells from the Koster Area (West Sweden, Figs. 27a-b) strongly support the synonymy. However the neotype of *C. pusilla* (NHML), instituted by BROWN (1979: 216) on a British specimen, was not examined by the writers. We found that the figures and descriptions of British shells identified as *C. pusilla* by GARSTANG (1894: pl. XLIV, figs. 4a-b), and by BROWN (1979: 207; 205, fig. 1c) may leave in doubt about their identity, if compared with the mentioned Scandinavian shells (also T. Schiøtte, personal communication).

CECALUPO & GIUSTI (1989: 99; 102, fig. 5) already recorded *C. pusilla* for the Mediterranean, and Mediterranean material of *C. pusilla* is kept in the SMNH, Stockholm, and MNHN, Paris (SCHIØTTE, 1998: 130). *C. pusilla* is not rare in the Tyrrhenian Sea: we have examined some shells from the Strait of Bonifacio (between Corsica and Sardinia), the Tuscan Archipelago, and off Civitavecchia (Lazio,West Italy) (I. Nofroni coll.; LPT coll.). «*Diaphana quadrata* (Monterosato, 1874)» sensu NORDSIECK (1972: 25; 235, fig. 4) seems not to be this species, but probably a small member of the genus *Diaphana* T. Brown, 1827, similar to *Diaphana cretica* (Forbes,1844) (SCHIØTTE, 1998: 125-126; 123, figs. 24D, E, I, J), possibly being a dwarf form of the latter with a small protoconch, or a still undescribed species (in study by LPT: cf. OLIVERIO, 2000: 47, fig. 12).

Familia RETUSIDAE Thiele, 1931

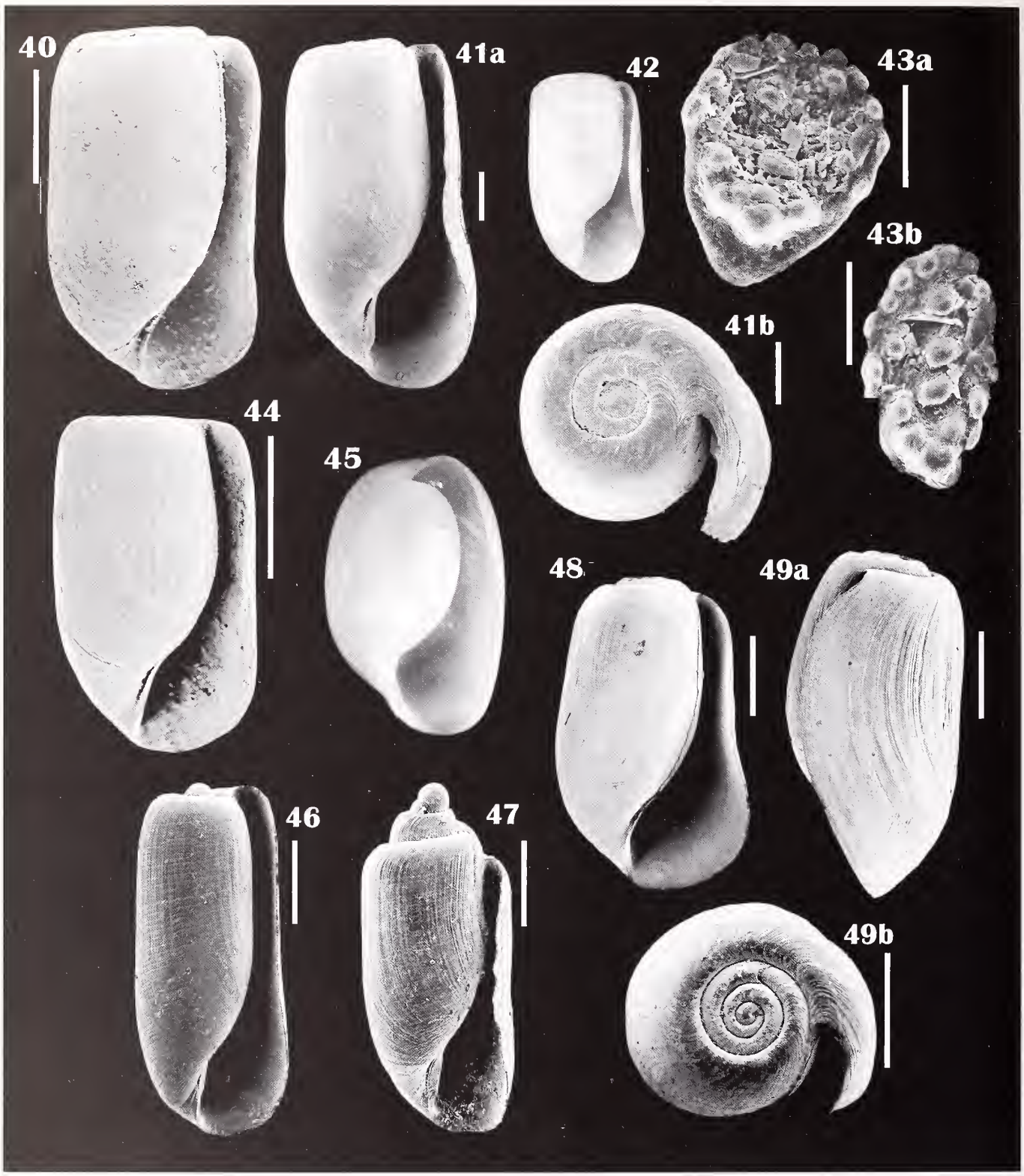
***crebrisculpta*, *Cylichnina* Monterosato, 1884**

First valid introduction - MONTEROSATO (1884: 143 \799\) by means of a description.

Type material - Two shs from Palermo (Sicily), unrecorded depth (Figs. 28, 29, 50). The original label and box were lost, arguably during the Exhibit in 1976, (the box's number should be 16017). A manuscript note on a copy of the catalogue of the Exhibit and a label both by hand of a Curator of the Exhibit (apparently G. Schirò) identify them as being *Cylichnina crebrisculpta*, collected at Palermo, from the Monterosato coll., box 16017.

Remarks - The material of *Cylichnina crebrisculpta* now kept in the Monterosato's collection includes only the mentioned shells, used for the Exhibit in 1976. The original label has not been found, being probably lost during the preparation of the Exhibit. However these shells should come from the Monterosato coll. (box 16017) having as locality Palermo, according to the mentioned notes. Both syntypes are damaged and not very fresh. One shows a bore hole, whereas the other is slightly broken on the parietal side of the aperture. Both shells match well enough the original description, as well as the illustrations given by a well-known correspondent of the Marquis (DAUTZENBERG, 1891: pl. XVI, figs. 1-2). Of the material from Cape San Vito and Naples, mentioned by MONTEROSATO (1884) after Palermo, there is no trace.

The actual distinction of the Eastern Atlantic-Mediterranean *Retusa* species with sunken spire, apical umbilicus, and spiral lines, is problematic. These are frequently ascribed to the (sub)genus *Cylichnina* Monterosato, 1884, which the writers simply consider a synonym of *Retusa* T. Brown, 1827, and include the following



Figs. 40-44: *Retusa minutissima* - Fig. 40: Paleohora (Crete Is.), bioclastic sand sample 10 m (S. Farinelli legit, LPT coll.); Figs. 41-42: syntypes of *Utriculus minutissimus*, Algiers, 15 m (P. Joly legit) (Fig. 42, h.: 1.4 mm); Fig. 43a-b: gizzard plates (Fig. 43a: unpaired pl.; Fig. 43b: paired pl.), Valencia (Southeast Spain) (Monterosato coll.); Fig. 44: Cala Iris (Torres de Alcalá, Mediterranean Morocco), bioclastic sand sample 10 m (R. Villa legit, LPT coll.). **Fig. 45**: *Haminaea hydatis* (Linné), holotype of *Haminoea hydatis* var. *cymoelium*, Bengasi (h: 10.5 mm). **Figs. 46-47**: *Retusa mamillata* (Philippi), shells with nearly sunken or protruding spire, Stn. AKD.92-No. 22, Kash (Turkey), bioclastic sand sample 34 m (AKDENIZ exp., 1992, Univ. "La Sapienza", Rome). **Figs. 48-49a-b**: *Retusa obtusa*, Le Verdon-sur-Mer (Aquitanie, Western France), typical form with flat spire (F. Settepassi coll., ZMR). **Scale bars**: 1.0 mm (48, 49ab); 500 µm (40, 44, 46, 47); 200 µm (41a-b); 50 µm (43a-b).

nominal species: *Retusa strigella* (Lovén, 1846) (Fig. 30), *R. laevisculpta* (Granata-Grillo, 1877), *R. crebrisculpta* (Monterosato, 1884), *R. crossei* (B.D.D., 1886), *R. variabilis* Milaschewith, 1909, *R. ovoides* (Milaschewich, 1916), *R. multiquadrata* Oberling, 1970, and possibly *R. umbilicata* (Montagu, 1803). On this question the type material of *C. crebrisculpta* does not throw any new light.

Noteworthy, MONTEROSATO (1890: 189 \923\) changed his view later on, quoting *crebrisculta* as a synonym of *Retusa strigella* (Lovén, 1846) [*Cylichna*]. This fact is even more surprising since Monterosato was becoming more and more a splitter in that period. Anyway he was possibly right: it is difficult to find any feature really useful to distinguish the type material of *crebrisculta* from the more slender shells of *Retusa strigella*, with the exception of a moderately stronger sculpture, more similar to *Retusa laevisculpta* (Granata-Grillo, 1877). The identification of *Bulla umbilicata* Montagu, 1803, with *strigella* is commonly stated in recent literature, yet not proved, possibly *umbilicata* corresponding to the non-striated *Retusa nitidula* (Lovén, 1846). For this reason, we prefer to adopt the name *strigella*.

effusa, Coleophysis **Monterosato, 1890**

First valid introduction - MONTEROSATO (1890: 188-189 \922-923\) by means of a description.

Type material - Five shs. (Figs. 31, 32, 52), badly preserved, from Palermo (Sicily), unrecorded depth, certainly from deep water (original label: «n. sp.? Palermo 1886»), from the box 16030.

Remarks - MONTEROSATO (1890: 188 \922\) introduced the species in a work on the deep water molluscs of Palermo, yet quoted also a lot from Villefranche (South France), sent by S. Hanley. Actually, there is no material labelled as *Coleophysis effusa* in the Monterosato coll. Therefore we have been compelled to check all the lots of small opisthobranchs trying to find what could reasonably be regarded as type material of *C. effusa*. We found in the box 16030, mostly containing lots labelled as *Retusa truncatula* (Bruguiére, 1792) and *R. semisulcata* (Philippi, 1836), a tube with *R. truncatula*-like shells, arguably from deep water - a shell still holds a *Limacina retroversa* (Fleming, 1823) stuck in the aperture - labelled as «n. sp.? Palermo 1886» by hand of Monterosato. The dating 1886 shows that it was collected after MONTEROSATO (1884), where *C. effusa* was not mentioned, and before the description in 1890. The origin fits *C. effusa*. Moreover the material corresponds well enough to the original description – very concise indeed - of *C. effusa*, and Monterosato was inclined to consider these shells as belonging to a new species, as shown by the label. These considerations allow to conclude that the description of *C. effusa* was based on this material - at least in part. The lectotype shows a somewhat damaged peristome, however it is better preserved than the other material. A further tube in the box 16030, containing a shell from Villefranche, does not match the remark by MONTEROSATO (1890) because it was collected by J.T. Marshall, not by Hanley. It is likely that the material of Monterosato, despite being collected in moderately deep water, came from shallow bottoms – other species listed by MONTEROSATO (1890) are in fact shallow water ones. The record of *C. effusa* by LOCARD (1905: 58) was based on shallow water material (10-90 m).

Based on this material, *Coleophysis effusa* seems, at least from shell morphology, a weakly sculptured form of the variable *Retusa truncatula* (cf. Figs. 33, 34, 58) with a small size, possibly close to the form "*pellucida*" T. Brown, 1827. It is hard to say whether *effusa* could represent merely a form, or a distinct species within the probable complex of *Retusa truncatula*, all this group being poorly known.

minutissimus, Utriculus **Monterosato, 1878, ex H. Martin MS.**

First valid introduction - MONTEROSATO (1878b: 159 \449\) by means of a description.

Type material - Eleven spms./shs. (Figs. 41a-b, 42) from Algiers (Algeria) 15 m, from box no.16015 (P. Joly legit; original label: «*Utriculus minutissimus* Martin Algiers 15 m.» by hand of Joly); 146 spms./shs. from Algiers (Algeria), unrecorded depth, (P. Joly legit); 27 spms. (Figs. 38a-b, H. Martin legit); Gulf of Fos (Southern France), unrecorded depth, 7 shs. (G. Doria legit), Vado, near Genova (Liguria, Northwestern Italy), unrecorded depth,; 1 sh. (Caifassi brothers legit), Livorno (Tuscany, Western Italy), depth unrecorded on the label - yet about this lot, MONTEROSATO (1878b: 159 \449\) wrote: «profondeur de 30 métres, par un fond de vase fine et jaunâtre»). All the examined syntypes are kept in the box 16015.

Remarks - Before the original description Monterosato had quoted the species as *Utriculus obtusus* var. *minor*, *Cylichna minutissima* H. Martin MS., *Utriculus minutissimus* H. Martin MS., and *Utriculus obtusus* var. *minor, apice depresso* Jeffreys, all nomina nuda (MONTEROSATO, 1872: 54 \136\; 1875: 46 \272\; 1878a: 110 \424\). Although the description is included in a work on the marine molluscs of Palermo, no material labelled as from Palermo was found by the writers. We have regarded as syntypes all the material from localities and/or senders quoted just below the original description, or in previous works - Gulf of Fos, Vado, Livorno, harbour of Algiers. On the bottom of the box 16015 it was found a label by hand of Monterosato: «*Utriculus minutissimus*, H. Martin MS. = *U. obtusus*, var. *minor, apice depresso*, Jeffr. varie località!», now kept with the types. A young shell of *Retusa truncatula* (Bruguière, 1792) is mixed within the syntypes from Algiers, unrecorded depth.

There are further lots in the Monterosato coll., apparently obtained after the original description – some of these localities are quoted in MONTEROSATO (1884: 142 \798\). Therefore we do not regard them as type material. They are: from box 16015: 168 spms./shs., Valencia (Southeast Spain), unrecorded depth; 67 shells, Cagliari (South Sardinia), unrecorded depth,; (h) 14 shells, Smirne [= Izmir] (West Turkey), unrecorded depth (Terquem legit); from box 16019: 5 shells Algiers (in a tube the sender is specified: «Joly»), unrecorded depth, (labelled by Brugnone); 1 fossil shell, Ficarazzi (Palermo, Sicily), probably from Pleistocene deposits (labelled by Brugnone). There is also a tube from Cape San Vito (West Sicily) erroneously identified - two small *Cylichnina*-like shells. On the bottom of the box there is a label on which some locality is pointed out:

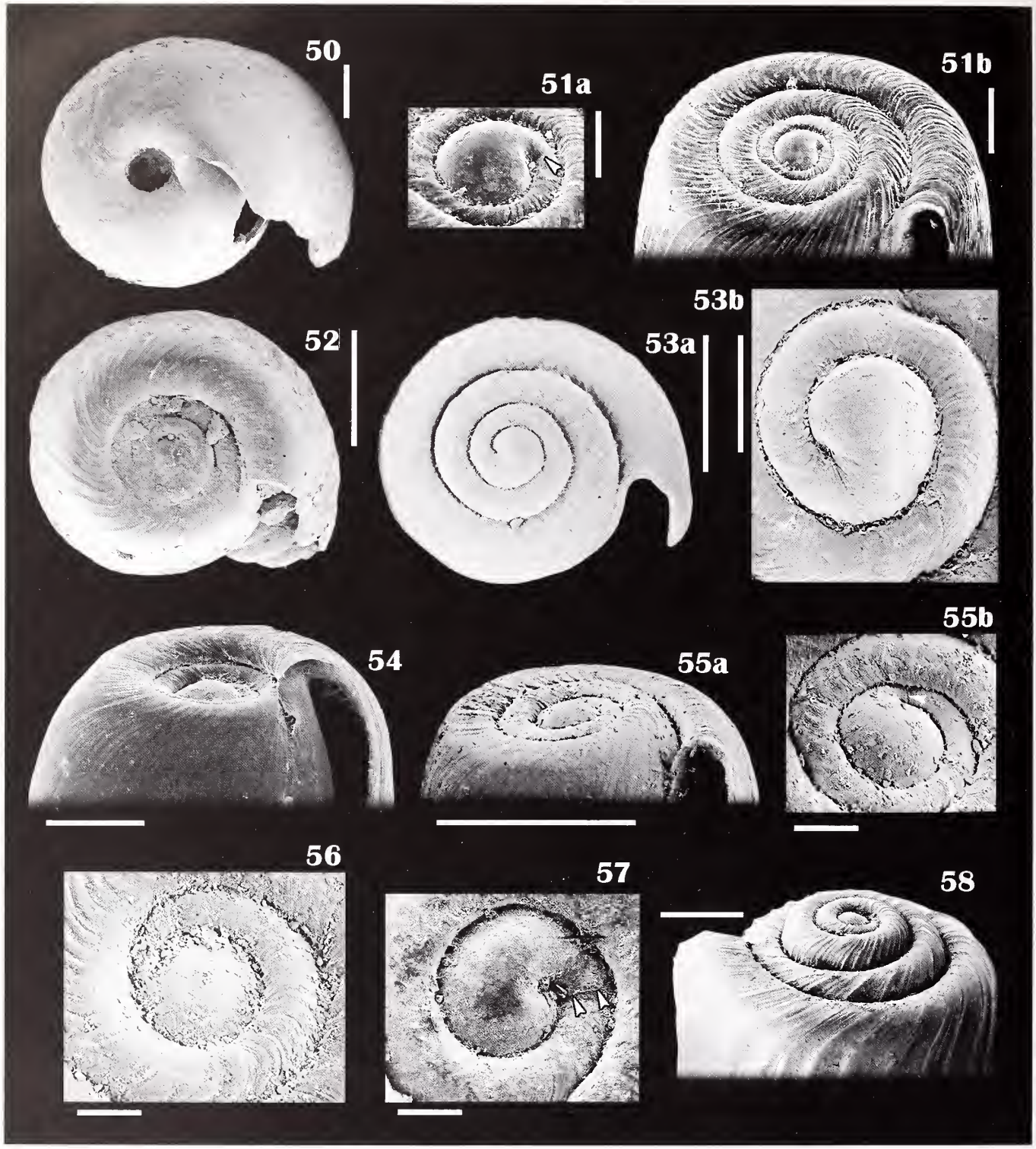


Fig. 50: *"Cylichnina crebriscalpta"*, syntype, Palermo, upper view. **Figs. 51a-b:** *Retusa leptoeneilema* (Brusina), Umag, Dalmazia, beached, protoconch and shell top. **Fig. 52:** *Retusa truncatula* (Bruguière) [s.l.], syntype of *Coleophysis effusa*, Palermo, upper view. **Figs. 53a-b:** *Retusa obtusa* (Montagu) [s.l.], form apparently corresponding to *Bulla pertenuis* Mighels, Killala Bay (Donegal Bay, Northwest Eire), beached, upper view and protoconch. **Figs. 54-56:** *Retusa minutissima* - Fig. 54: Valencia (Southeast Spain), shell top with sunken spire; Figs. 55a-b: Paleohora (Crete Is.), shell top and protoconch; Fig. 56: Cala Iris (Torres de Alcalá, Mediterranean Morocco), protoconch. **Fig. 57:** *Retusa obtusa* [s.l.], Le Verdon-sur-Mer (Aquitanie, West France), typical form with flat spire, protoconch. **Fig. 58:** *Retusa truncatula*, f. with protruding spire, Djerba Is. (Tunisia), shell top. **Scale bars:** 500 µm (52, 53a, 55a, 58); 200 µm (50, 51b, 53b, 54); 100 µm (51a, 55b, 56, 57). - (Arrows on Figs. 51a, and 57 point to the protoconch–teleoconch boundary).

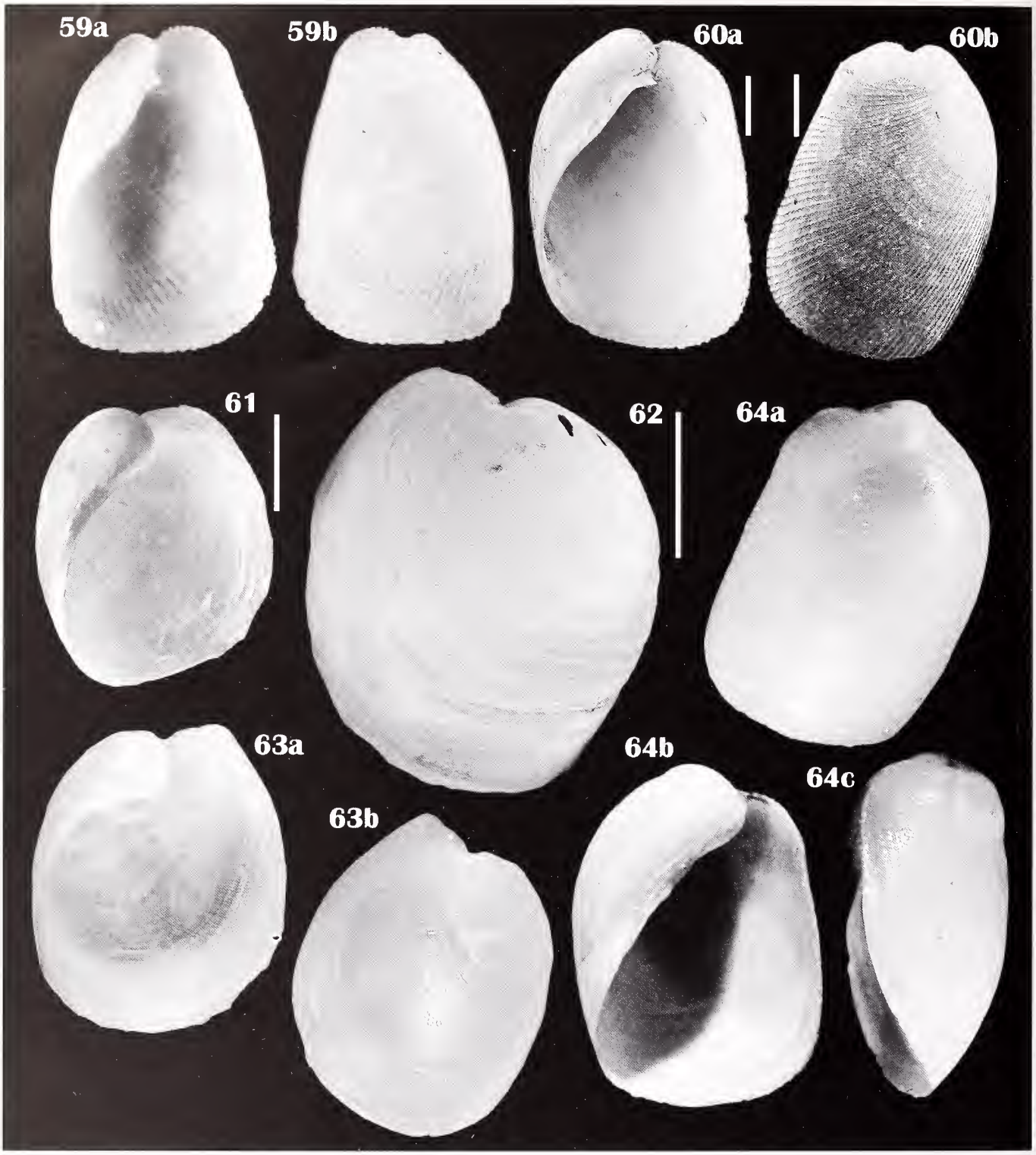
«Trap. ["Trapani"], Viareggio, Alger, S. Vito». The shells from Algiers could be from the same sample of the syntypes (Algiers), sent to Brugnone by Monterosato, and later on returned to Monterosato along with the rest of the Brugnone coll., but there is no clear evidence of this and, therefore, they are not regarded as type material here. Finally in the box 16014 we found: a tube with 9 poorly preserved shells from Trieste (Northeast Italy, Adriatic Sea), 10 fms (= 18.5 m ca.) labelled by an unidentified hand.

This species is widespread in the whole Mediterranean Sea, and it may be locally common. In the past *Utriculus minutissimus* was recorded for several Mediterranean localities (see, e.g.: Locard, 1892: 29; Locard & Caziot, 1900: 26; Coen & Vatova, 1932: 26; Van Aartsen *et al.*, 1989: 68; Bogi & Galil, 1997: 43). We have also examined further material 4 shs, Cala Iris (Torres de Alcalá, Mediterranean Morocco), sediment 2-10 m (Figs. 44, 56); 2 dry spms, Valencia (Southeast Spain). (Figs. 36, 37, 43a-b, P. Pallary legit), F. Settepassi coll. (ZMR); 3 shells, Paleohora (Crete), sediment 10 m (S. Farinelli legit; Figs. 40, 55a-b); 3 shells, Datcha (Southwestern Turkey), unrecorded depth (R. Villa legit; E. Talenti legit) The species was also recorded for the Atlantic waters, near the Strait of Gibraltar by Pallary (1902: 6; 1920: 20). It seems to inhabit detritic-muddy bottoms on the continental shelf. As previously noticed it is known also as fossil from Sicily.

Nordsieck (1972: 36), as well as all the recent check-lists of Mediterranean marine molluscs (Piani, 1980: 159; Bruschi *et al.*, 1985: 33; Sabelli *et al.*, 1990-92: 53, 424; see also Bedulli *et al.*, 1995: 6) adopted the genus *Pyrunculus* Pilsbry, 1895, for *Utriculus minutissimus*. On the other hand, Pallary (1902: 6; 1920: 20), Coen & Vatova (1932: 26), Settepassi et al. (1976: 26), Van Aartsen *et al.* (1989: 68), Gaglini (1991: 6), Tringali (1993: 26), and Bogi & Galil (1997: 43) regarded this species as a member of the genus *Retusa* T. Brown, 1827, a position which we share. The shells of *Pyrunculus* are characterised by a more or less pyriform outline (Pilsbry, 1895a: 229; Thiele, 1931: 389; Bouchet, 1975: 333), whereas *Utriculus minutissimus* has an evenly cylindrical shell, similar to those of many other *Retusa* species. Monterosato (1878b: 159-160) described this species in the genus *Utriculus* T. Brown, 1844 - a synonym of *Retusa* – comparing it with *Retusa leptoeneilema* (Brusina, 1866), a closely similar species with a rather cylindrical shell too. The gizzard plate morphology confirms this systematic position showing typical *Retusa* characters: they are small, corneous, subtriangular in shape, slightly curved, with many small tubercles spread on the surface, darker in colour than the light brown background (Figs. 43a-b) (cf. Tringali & Oliverio, 2001, this volume). «*Pyrunculus minutissimus* ([H. Martin] Monterosato, 1878)» *sensu* Nordsieck (1972: 36; 237, fig. 15) may be a true *Pyrunculus*, yet it does not share *Utriculus minutissimus*' shell morphology.

Utriculus minutissimus has been occasionally regarded as a distinct species - see, e.g., the previously quoted references, as well as Carus (1893: 184) and Locard (1905: 60). Frequently, it has been considered as a dwarf form of the Atlantic *Retusa obtusa* (Montagu, 1803), expecially by Northern authors. This view probably spread under the eminent influence of Jeffreys (1870: 20), who pointed out the occurrence of a variety *minor, apice depresso* of *Utriculus obtusus* (Montagu, 1803) in the Mediterranean Sea. Monterosato (1878b) underlined that this form is the same of *Utriculus minutissimus*. *Retusa minutissima* has a cylindrical shell very similar to *R. obtusa* (Figs. 39a-b, 48, 49a-b, 53a-b, 57), having only a weak sculpture of growth lines - rarely developing in exceedingly weak ribs on the upper part of some shells - and an usually flattened spire. In fact, the spire of both species shows a wide range of protrusion-immersion degree, from shells with well prominent, *Actaeocina*-like whorls, to others with a nearly concealed, *Cylichnina*-like spire (cf. Figs. 36, and 37). Although *R. obtusa* is similar to *R. minutissima*, it may be distinguished by a set of characters. The teleoconch of *R. obtusa* is larger, shells with a height of 5-6 mm being not rare, whereas *R. minutissima* is very tiny, with a height of about 1.0-1.2 mm, only occasionally attaining to 1.5 mm. Its outline is less cylindrical than *R. minutissima*, slightly more rounded, more or less swollen toward the base, especially if large shells are taken in account. Its suture is deeper. The growth lines seem slightly more rounded, as is the peristome observed in lateral view. The columellar callus of both species is thin, yet proportionally more in *R. obtusa* and is more evenly curved. The part of the protoconch of *R. obtusa* not concealed by the first teleoconch whorl is usually more prominent from the spire, and its diameter (about 0.20-0.23 mm) is larger than that of *R. minutissima* (0.15-0.17 mm) (cf. Figs. 53b, 57, and 55b, 56). In fact, the protoconch of *R. obtusa* is larger than that of any Mediterranean *Retusa* species we know. A large larval shell is not surprising since *R. obtusa* is known to lack a planktotrophic larval phase (Smith, 1967: 760-762). According to Jeffreys (1867: 423), fresh shells of juvenile *R. obtusa* are sculptured by microscopic spiral lines. We were unable to notice this feature on the juvenile shells of *R. obtusa* available to us from the Northwest Atlantic (Bay of Biscay, Northwest Ireland, and West Sweden), perhaps not fresh enough to preserve the weak sculpture. Fine and close-set spiral lines are present on the shells of *R. obtusa* s.l. in a lot from the Behring Sea (LPT coll.). These shells are probably adult, and perhaps correspond to "*Bulla*" *semen* Reeve, 1855: the problematic identity and relationship of this taxon with *R. obtusa* were discussed by Lemche (1948: 53-54). The spiral sculpture was quoted also by Pruvot-Fol (1954: 86), Nordsieck (1972: 33), and Rehder (1988: 644): it is likely, however, that they simply quoted the remark by Jeffreys (1867). Anyway, *R. minutissima* lacks any kind of spiral sculpture. Although Lemche (1948: 51-53; 84-86) and others listed several names as synonyms of *R. obtusa*, it is very likely that *R. obtusa* is in fact a complex of species. This species lacks a planktotrophic larval stage, and therefore its allegedly very wide distribution, ranging from the Northeastern Pacific, and the Eastern coast of North America to the Eastern Atlantic Ocean, and the Mediterranean Sea, is possibly questionable. *Retusa minutissima* may be regarded as a species of this group not difficult to distinguish even basing the shell morphology alone.

A further closely similar species is *Retusa leptoeneilema* (Brusina, 1866), known with certainty from the Central and Eastern Mediterranean basins (Figs. 34, 48a-b). This species shares with *R. minutissima* a rather flat spire, an evenly cylindrical shape, and the absence of any spiral sculpture. Moreover, the exposed part of the protoconch of *R. leptoeneilema* seems identical to that of *R. minutissima*. It is not always easy to distinguish shells of these species, however *R. leptoeneilema* has a thicker and larger teleoconch, usually attaining 1.5-3 mm of h, and usually bearing a more evident axial sculpture - weak and sharp axial ribs vanishing toward the base. Shells of *R. leptoeneile-*



Figs. 59-60: *Philine intricata*, syntypes, Palermo (Figs. 59a-b, h: 3.5 mm). **Figs. 61-63**: *Philine monterosati*, Fig. 61: Termini Imerese (Sicily), unrecorded depth (Monterosato coll.); Fig. 62: syntype, Palermo; Figs. 63a-b: Vibo Marina, muddy bottom, 400 m ca. (h.: 7.2 mm; from a preserved animal with a lenght: 13 mm. ca.) (R. Ardovini legit, LPT coll.). **Figs. 64a-c**: *Philine quadrata* (S.V. Woods), Kristiansand (Norway), unrecorded depth (h: 5.6 mm) (Monterosato coll.). **Scale bars**: 2.0 mm (61, 62); 500 µm (60a-b).

ma with a very weak axial sculpture, similar to *R. minutissima*, may occasionally be found, but usually are worn shells, probably smoothed by rolling within the sediment. Moreover *R. leptoeneilema* shows a thicker columellar callus, usually with a blunt nodular fold, evident also on juveniles. Its suture is more deeply incised, and its basal umbilical chink is slightly larger. The spire of *R. leptoeneilema* is less variable than *R. minutissima*, not displaying a wide range of protrusion-immersion degree, being almost always evenly flattened.

Van Aartsen & Kinzelbach (1990: 110) considered *R. minutissima* a small form of *Retusa truncatula* (Bruguière, 1792). Yet it seems that there are no intermediate forms between *R. minutissima* and *R. truncatula* (Fig. 33). On some shells of *R. truncatula* the upper part of the body whorl is slightly lower than the spire. Therefore the spire of this form, though more or less flattened, is slightly protruding above the body whorl. Specimens of this form are not rare at Djerba Is. (Tunisia), where the species attains a somewhat large size (h: 3-5 mm) (Fig. 32), and may be occasionally found in other areas. However all the other features allow to discriminate these form of *R. truncatula* from both *R. minutissima* and *R. leptoeneilema*. *Retusa mamillata* (Philippi, 1836) has a characteristic shell, with a very variable spire (Figs. 44, 45), and evident spiral lines on the teleoconch: it cannot be misidentified with *R. minutissima*. Noteworthy, *R. mamillata* is a full valid species, not a form of *R. truncatula*, although some authors (e.g. Lemche, 1948: 55) considered it as a synonym of the latter.

Familia HAMINOEIDAE Pilsbry, 1895

***cymoelium*, *Haminoea hydatis* var.** Monterosato, 1923

First valid introduction - Monterosato (1923: unnumbered pl. \1317\, fig. 16) by means of a named figure (an indication).

Type material – The holotype (Fig. 45) is a sh. glued on a stick of paper, from Bengasi (Lybia), (C. Crema legit), unrecorded depth (arguably beached: cf. Monterosato, 1923: 3 \1308\)labelled by hand of Monterosato as: «*cymelium* typ. Monts. Bengasi!! Fig.16», box 16253.

Remarks - Nordsieck (1972: 32) raised this variety to the rank of subspecies, thus making the name available (ICZN 1999: Art. 45.6.3, 45.6.4, and Art. 45.6.4.1). The shell is clearly the same photographed by Monterosato (1923). The type locality is obviously Bengasi (Lybia). Despite that recent works on Northeast Atlantic-Mediterranean *Haminoea* species show how scanty is the significance of shell morphology in specific systematics of this group, we notice that the holotype of *Haminoea cymelium* seems to be a faded, worn shell of *Haminoea hydatis* (Linné, 1758).

Familia PHILINIDAE J.E Gray, 1850

intricata*, *Philine Monterosato, 1884

First valid introduction - Monterosato (1884: 147 \803\) by means of a description (see below).

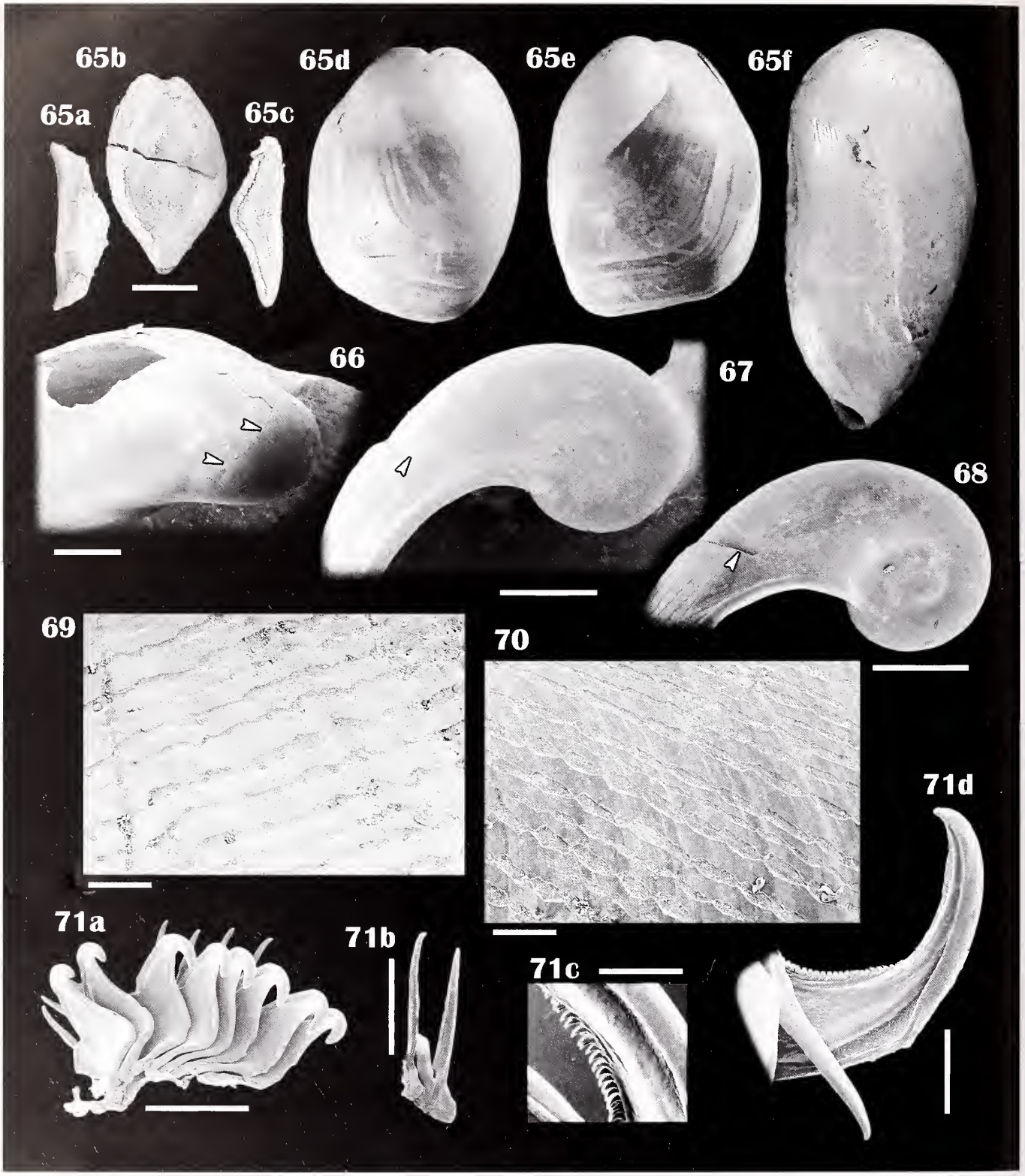
Type material - 28 shs., plus some frgs., Palermo, from the box 16301 (original label: «*Philine intricata*, Monts. Palermo!») (Figs. 59a-b, 60a-b). Gaglini did not select a lectotype (see Gaglini, 1991: 12; 20, unnumbered figs.), yet she gave the syntype of Figs. 59a-b a separate place in the original tube, arguably regarding it as the better syntype for a future selection.

Remarks - Monterosato (1884) first validly introduced this name, though without any reference to a locality. In some previous work *Philine intricata* is published as a nomen nudum accompanied by some locality - Monterosato. (1875: 47 \273\): Palermo 60-90 m; Monterosato. (1878a: 111 \425\): from Palermo and Trapani 60-90 m; Messina (Granata-Grillo); Algiers (Joly); Monterosato (1878c: 319 \459\): Algiers. Only one of the quoted localities is now represented in the Monterosato coll., namely Palermo. The material from other localities examined by us evidently was included in the collection later, being not type material: 2 shells, large for the species and well-preserved, from St. Raphael Is., Azores Islands, 50 m; 1 shell, small and badly preserved from Naples; both lots in box 16301. In a monographic paper on *Philine intricata*, Van Der Linden (1994) does not mention further type material from other public collections, which, however, may exist.

Giannuzzi-Savelli & Piani (1990: 173) considered invalid this taxon in Monterosato's works judging insufficient as a description Monterosato's (1875) few words on this species - «*P. intricata*, Monterosato nov. sp. C. Palermo 60-90 m! Prossima ma distinta, secondo Jeffreys, alla *Philine lima*, (*Utriculus*) Brown = *Bulla lineolata*, Couthouy, ch'è artica», *viz.*: "*P. intricata*, Monterosato new species, coralligenous, Palermo 60-90 m, directly examined by Monterosato. In Jeffreys' opinion closely similar to the Arctic *Philine lima*, (*Utriculus*) Brown = *Bulla lineolata*, Couthouy, yet distinct". Actually, Monterosato (1875) is not a description, but the simple reference to a resemblance with *Philine lima* (T. Brown, 1827), not itself a diagnostic character of the species. Despite Monterosato (1875) was considered as the valid introduction of the name by others (Settepassi *et al.*, 1976: 25; Piani, 1980: 161; Bruschi *et al.*, 1985: 34; Giannuzzi-Savelli, 1989: 1578; Sabelli *et al.*, 1990-1992: 54, 232, 426; Gaglini, 1991), this view seems untenable.

However, as already noticed by Van Der Linden (1994: 42), there is the description by Monterosato (1884) to make available the name *Philine intricata*. This description is nearly telegraphic: it simply remarks that a new section of the genus *Philine* Ascanius, 1772, could be introduced for this species «che ha la columella sinuosa e canalicolata come nel genere *Raincourtia*, Fischer [...]», viz. "which has a sinuous and channelled columella as in the genus *Raincourtia*, Fischer [...]" (on *Raincourtia*, see Fischer, 1884). Nevertheless, it describes a character of the species, thus it satisfies the ICZN (1999: Art. 12.1), making the name available. The most characteristic feature of the shell of *P. intricata* is actually that underlined by its original description, namely the flexuous columella, with an evident fold. Its outline is also more squared than the similar *Philine catena* (Montagu, 1803), it is flatter in lateral view, and its peristome more coarsely serrated.

This species was omitted in the comprehensive manuals by Kobelt (1895-1896), and by Pilsbry (1895b). More generally, it was overlooked by the malacological literature, until its recent rediscovery by Gaglini (1991), who also figured a syntype of the Monterosato coll. (here Figs. 59a-b), and the careful description by Van Der Linden (1994), who also provided further data on its distribution, and good SEM photos. Nothing is still recorded in literature about the soft parts and/or its ecology. Yet, it is noteworthy that «*Philine catena* (Montagu)» *sensu* Vayssière (1885: 35-38; pl. 1, figs. 25-34) seems to be this species, at least in part, as it is shown by the folded columella of the figured shell: therefore the anatomical characters described there could be ascribed, at least in part, to *P. intricata*. If this is right the radular formula would be 1.1.0.1.1, and the



Figs. 65a-f: *Philine monterosati*, syntype, Palermo; Figs. 65a-c: gizzard plates; Figs. 65d-f: shell. **Figs.** 66-67: *Philine monterosati*, syntype, Palermo, protoconch, in lateral and lower view, respectively. **Fig.** 68: *Philine quadrata* (S.V. Wood), West Sahara, 24°-25° N lat., 40-60 m, gastric contents of flatfish (fam. Pleuronectidae), protoconch in lower view (F. Gubbioli legit, LPT coll.). **Figs.** 69-70: *Philine monterosati*, detail of sculpture on the central part of the body whorl - Fig. 69: syntype, Palermo; Fig. 70: subadult shell, Civitavecchia (West Italy), inside an old Roman amphora, 550 m ca.) (R. Ardovini legit, LPT coll.). **Figs.** 71a-d: *Philine monterosati*, details of the radula, Vibo Marina (same spm. as in Figs. 63a-b) - Fig. 71a: a portion of the radula; Fig. 71b: marginal teeth; Fig. 71c: detal of the denticulation on a lateral tooth; Fig. 71d: lateral and marginal teeth. **Scale bars:** 1.0 mm (65a-c); 200 µm (66, 67, 68, 71a); 100 µm (69, 70, 71b); 50 µm (71d); 25 µm (71c) - (Arrows on Figs. 66, 67, and 68 point to the protoconch-teleoconch boundary).

species would show a gizzard with three plates, proportionally large, narrow and long, as that figured by the French author.

The species was recorded as a member of the Recent fauna of the Eastern Atlantic (Northwest Africa, Canary, Azores, Cape Verde Islands), and of the Western and Central Mediterranean, and, as a fossil, from the Pliocene of Belgium - see the above quoted works by MONTEROSATO, and VAYSSIERE (1885), VAN DER LINDEN (1994: 47-48; 1995), SYKES (1905: 324), and MORENO & TEMPLADO (1998). It seems quite clear that NORDSIECK & GARCÍA-TALAVERA (1979: pl. XLIII, fig. 16) published a drawing of *P. intricata* from the Canary Islands with the name «*Philine monterosatoi* (Vayssière, 1875)» – the authorship of *P. monterosati* has been a matter of discussion up to date (see below). Also the drawing of *P. monterosati* by NORDSIECK (1972: 233, fig. 13) seems in fact *P. intricata*. *Philine monterosati* and *P. intricata* are not very similar. The shell of *P. monterosati* is closer to *Philine quadrata* (S.V. Wood, 1839). It is far larger than *P. intricata*: the largest shells may attain a height of about 10 mm. Both its lateral and frontal outline are quite rounded and swollen; conversely *P. intricata* is somewhat squarish frontally, slightly restrained toward the top on the largest shells - with a height of about 3-4 mm - and it is very flat and subtriangular laterally. The evenly arched columella of *P. monterosati* lacks a fold, and its peristome is not serrated as *P. intricata*. The latter is usually found in shallow waters, whereas *P. monterosati* is a deeper water species. *Philine intricata* is frequently found along the Canarian coasts, possibly even more frequently than in the Mediterranean Sea (cf. VAN DER LINDEN, 1994; 1995).

monterosati, Philine **Monterosato, 1874, ex Jeffreys MS.**

First valid introduction - MONTEROSATO (1874: 281 \207\) by means of a description.

Type material - One spm. from Palermo, now consisting of the sh. and the gizzard plates (Figs. 65a-f), unrecorded depth, from a box employed during the Palazzo Braschi Exhibit (1976), without number, yet with two original labels («*Philine monterosati* Jeffr. Palermo!!» and «*monterosati* Pal.!!»), and a note on the tube's cork («P. 1874», viz. "Palermo 1874"); 4 shs. mostly damaged + several fragments (Figs. 62, , 66, 67, 69) in a tube, Palermo, unrecorded depth (labelled «*monterosati* Pal.!!»), from the box 16303.

Remarks - MONTEROSATO (1872: 55 \137\) quoted *monterosati* - as nomen nudum - from the Adventure Bank, 92 fms. (communicated by Jeffreys), and Palermo. In 1874 the species was described on the basis of a single spm. from Cape San Vito, and material from Palermo consisting of several empty shells and a few spms. Apart from the mentioned lots from Palermo, all other material hold at present in the Monterosato coll. (box 16303) is not regarded as type material: there are 4 shells labelled by Brugnone from Cape San Vito and Palermo possibly sent by Monterosato, and 1 shell labelled by Monterosato from Termini Imerese (Northern Sicily). On the bottom of the box 16303 there are two labels, one by Brugnone [«*Philine monterosati* Jeffr. Pal. (Dr.)»], and the other by Monterosato [«*Philine monterosati* Jeffr. varie località!»].

The authorship on the name *P. monterosati* has been ascribed to other authors in the past. All agree on the fact that Jeffreys did never validly introduced the name, nevertheless either VAYSSIÈRE (1885: 34-35; pl. 1, figs. 22-24), or SYKES (1905: 325; 324, fig. 1), were proposed or quoted as the actual author (PRUVOT-FOL, 1954: 67; BOUCHET, 1975: 358; WARÉN, 1980: 36; VAN DER LINDEN, 1995: 69; also NORDSIECK, 1972: 22, and NORDSIECK & GARCIA-TALAVERA, 1979: 171, ascribed the species to Vayssière though with the date «1875»). The original description by MONTEROSATO (1874) is brief, though less brief than his habits; nevertheless it is a valid one in the sense of the ICZN (1999: Art. 12.1), the first to make the name available. The type material of *P. monterosati* is thus that on which he based the description, kept totally or partially in the ZMR.

This species lives in the Northeast Atlantic and Mediterranean waters. It does not have, like some congeneric species of the same area, a wide bathymetric range, and is known to inhabit only relatively deep waters, namely the outer shelf and bathyal detritic-muddy bottoms. PRUVOT-FOL (1954: 67) briefly summarized the morphology of shell, radula and gizzard plates ; later BOUCHET (1975: 356-357; ibidem, figs. 19a-d; pl. 4, fig. j) described the radula (1.1.0.1.1), the gizzard plates, and the male genital apparatus, giving schematic drawings, and a photo of a shell from the Sykes coll. ("Porcupine" Expedition); a rather unclear photo of the shell was published also by BIONDI & DI PACO (1981: 279, fig. 12). Otherwise not very much is known on this species.

We figure herein the three gizzard plates of a syntype (Fig. 65a-c), somewhat damaged and attacked by butyric acid, and the gizzard, with its fresher plates, and the radular teeth of a specimen from off Vibo Marina (Calabria, Southwest Italy; R. Ardovini legit; Figs. 71a-d, 72a-j). The plates are whitish, with a light brown external layer of conchioline, more evident on the edges, and rapidly desquamating after dehydration. They are apparently calcareous, however we did not chemically test them. As noticed by PRUVOT-FOL (1954) and BOUCHET (1975) the lateral teeth are denticulate along the cutting edge. This character is frequent in philinid gastropods. The marginals are narrow, sharply stylus-like in shape. The animals preserved in alcohol are pale flesh coloured, with a slender subtriangular cephalic shield, long slightly less than a half of the total length.

The shell of *P. monterosati* may reach a medium-large size for the genus (the largest syntypes has a height = 11 mm, Figs. 65d-f) and is characterised by its rounded outline, not oblique. Also in lateral view it looks evenly rounded and slightly swollen. The chain-like rows of linked pits are very fine and close to each other on *P. monterosati*, frequently loosing their chain-like aspect on the large shells, especially on the dead ones, when the pits become more coalescent within slightly winding and irregular lines (cf. Figs. 69, and 70). This could explain why DAUTZENBERG (1891: 613) described the species as simply sculptured by close spiral lines. Although very similar to *Philine quadrata* (S.V. Wood, 1839), it is distinguished by a set of characters. *P. quadrata* lacks a gizzard and has a different radular formula (2.1.0.1.2) (RUDMAN, 1972: 172; the radula was drawn by SARS, 1878: anatomical pl. XII, fig.7). Its shell (Figs. 64a-c) is not so large, albeit is more solid. Its outline is less evenly rounded, being more oblique and squared in frontal view. Also laterally observed it appears less rounded, and shows the widest depth well above the medium heigth of the shell, not at about the medium

Figs. 72a-j: *Philine monterosati*, Vibo Marina; Fig. 72a: gizzard observed from the side of the paired plates (lenght: 6 mm ca.); Figs. 72b-d: unpaired gizzard plate, respectively internal, lateral and extetnal sides (h: 4.8 mm); Figs. 72e-g: paired gizzard plate, respectively intetnal, lateral and external sides (h: 4.2 mm); Figs. 72h-j: the other paited gizzard plate, respectively external, lateral and internal sides (h: 4.2 mm) - (From the same spm. as in Figs. 63a-b).

heigth as in *monterosati*. Its spiral sculpture is more distinctly catenoid even on large shells, and on very young specimens it is easy to notice that the pits are more rounded and larger in diameter. The columella of *quadrata* is less arched, and its penultimate whorl is taller than in *monterosati*. The protoconchs are very similar in size and shape (Figs. 66,67, 68). They do not belong to the group of congeneric species with coarsely sculptured protoconchs – e.g. *Philine intricata*, *P. catena*, etc. – the surface being apparently smooth.

striatula*, *Philine Monterosato, 1874, ex Jeffreys MS.

First valid introduction - MONTEROSATO (1874: 281 \207\) by means of a description.

Type material - Two shells (Figs. 75a-b) from Cape San Vito (Trapani, Western Sicily);1 partially preserved spm. + 12 shs. + some frgs. (Figs. 73a-c), from Palermo, Sicily, unrecorded depth (a «P.» is

marked on the tube cork, standing for "Palermo"); original labels: on the bottom of the box two labels: «*Philine incerta* n. sp. [illegible, covered by an other word] Palermo 30 m anche d'Algieri 40 m (Joly)» and «*Philine striatula*, Jeffr. Palermo e S. Vito!»; in the tube of the lot from San Vito «S. Vito».;. All the material was found in the box 16322.

Remarks - MONTEROSATO (1872: 55 \137\) recorded *Philine striatula* (as a nomen nudum), from Palermo. Later on he described the species in a paper on the molluscs of Cape San Vito (MONTEROSATO, 1874), remarking its origin from deep water. All the material of *P. striatula* was in the box 16322. There is material labelled as from Cape San Vito and Palermo, but a lot of 4 shells from Palermo is labelled «Pal. 1886», thus not being type material. A further vial, however, containing shells and fragments - a fragment belongs to *Philine angulata* Jeffreys, 1867 – displays a «P.» marked on the cork («P.» always stands for "Palermo"). Though lacking any inner label this lot is here regarded as type material. The lot from Algiers, 40 m, sent by Joly, mentioned on the bottom label, is apparently lost.

Despite having been ascribed in recent literature to the Familia Diaphanidae Odhner, 1914, genus *Colobocephalus* M. Sars, 1870, *Philine striatula* turns out to be an actual member of *Philine*. It is a full valid species, closely reminiscent of *Philine punctata* (J. Adams, 1800). The shell (Figs. 73a-c, 74a-b, 75a-b) is characterised by the a more slender outline and a protoconch more protruding than usual for the genus, as well as by very fine and close set chain-like rows of linked pits. Nothing is yet known about the animal, apart from the occurrence of few foraminiferans in the poor dry residues of the soft parts obtained from stomachs of flatfishes (Fam. Pleuronectidae), captured along the West African coast (F. Gubbioli legit).

Ordo THECOSOMATA Blainville, 1824

Familia PERACLIDAE Tesch, 1913

***diversa*, *Spirialis* Monterosato, 1875**

First valid introduction - MONTEROSATO (1875: 50 \276\) by means of a description.

Type material - Four shs. and a few fragments from Palermo, 210-280 m, from the drawer A-1, box 51 (original label: recto: «*Spirialis diversa* Monts. n. sp. Palermo 210-280 m!»; verso: «*S. diversa* Monts. Palermo 280 m!») (Figs. 76a-c).

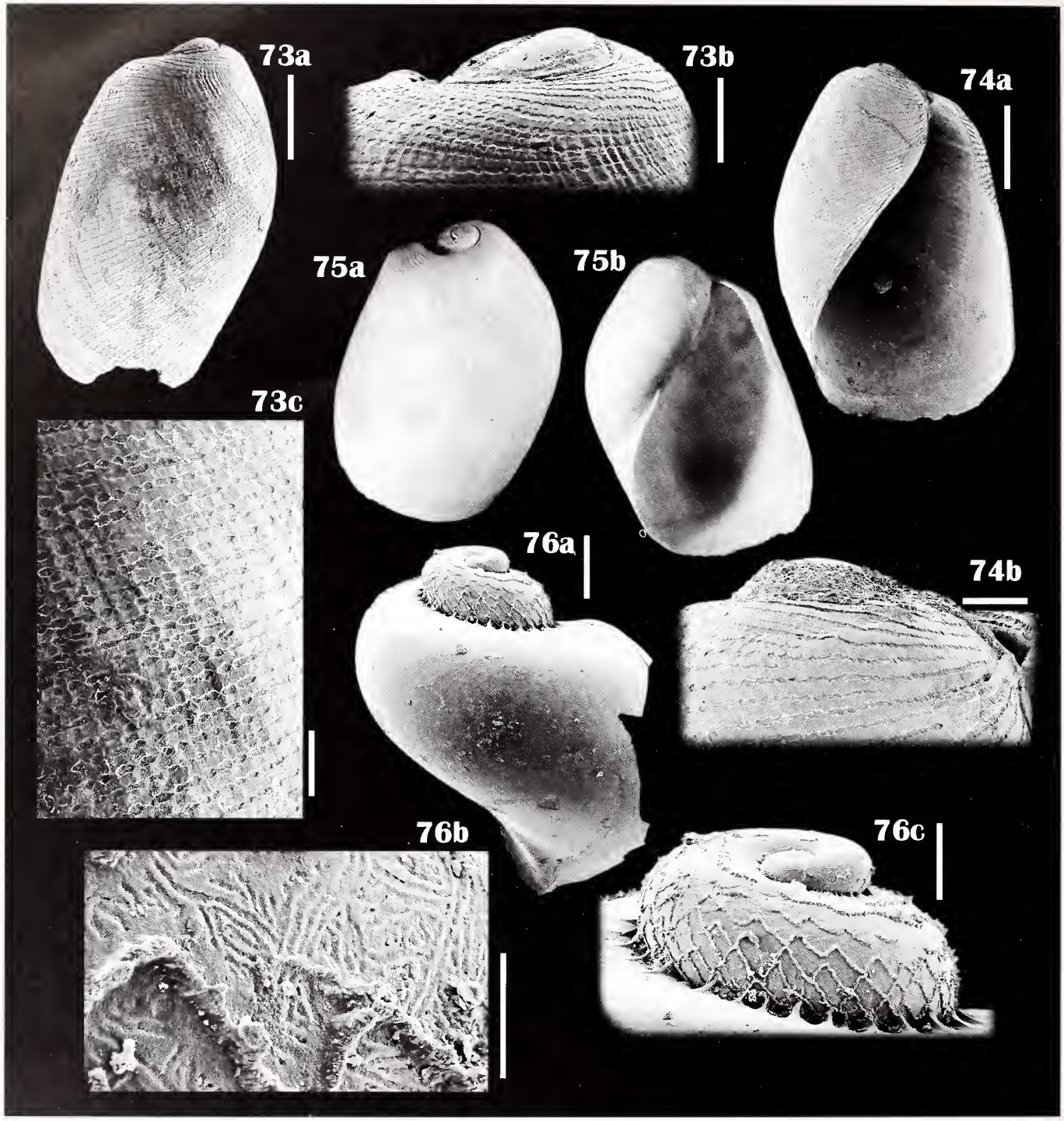
Remarks - MONTEROSATO (1875) described the shell as similar to *Spirialis reticulata* (d'Orbigny, 1836) (now *Peracle reticulata*) but with a less slender spire, a serrated suture, and a surface not covered by a network-like sculpture. He pointed out Palermo, 210-280 m, as provenance. The label in the tube of the syntypes matches with the depth noted below the description. The further material in the box 51 is more doubtful: the other lots do not contain labels, making doubtful their origin. Two labels on the bottom of the box read «*Peracle diversa* Monts. Palermo! Anche atlantica (Fischer)» and «*Peracl. diversa* Monts. Portogallo (Marshall)», respectively. These labels are obviously later than the original description, using also a new combination with the genus *Peracle* Forbes, 1844; therefore it may be concluded that the tubes without labels do not contain syntypes. GAGLINI (1991: 22, unnumbered fig.) photographed a syntype (a shell with a height = 1.4 mm) from the Monterosato coll., and the original label. Despite she seems to point out the occurrence of more material in the Monterosato coll., yet few shells are conserved now. Two further shells from the Monterosato coll. were figured by GAGLINI & VILLARI (1994: 308, the two shell on the upper row), together with the original label, being probably two syntypes too.

VAN DER SPOEL (1976: 29-30) judged *Spirialis diversa* Monterosato as a probable nomen nudum, but considered it as the same of *Peraclis bispinosa* Pelseneer, 1888. However the name by Monterosato is available (ICZN, 1999: Art. 12.1) since its telegraphic yet effective description of 1875, which points out the main characters of the shell. GIOVINE (1988: 24), GAGLINI (1991: 14; 22, unnumbered figs.), and GAGLINI & VILLARI (1994) concluded that *Peracle diversa* should be regarded as a senior synonym of *Peracle apicifulva* Meisenheimer, 1906, rather than *P. bispinosa*, a view shared by us. The major morphological feature is the same for *P. diversa* and *P. apicifulva*, namely the serrated suture, quite characteristic and usually evident also on worn or damaged shells We have scored at the SEM many irregularly shattered spiral lines, less evident, arranged among the main lines which sculpture the surface as a so called "Van Dyck pattern" (Fig. 76b). The wide distribution of this species in temperate and warm waters is summarised by means of a map by VAN DER SPOEL (1976: 408, fig. 170, as «*P. apicifulva*»). Its living occurrence in the Mediterranean waters is still to be confirmed (BEDULLI *et al.*, 1995: 23), the shells from Mediterranean sediments possibly belonging to the late Pleistocene.

Opisthobranch specific names not of Monterosato

A few opisthobranch specific names have been erroneously ascribed to the authorship of Monterosato in some works. A part of these names are in fact nomina nuda in Monterosato's works, or even simple nomina in schedis, yet others have no relation to the Marquis at all. Here we have tried to summarise as completely as possible these erroneous attributions as follow:

- *detruncata*, *Tornatina* as of Monterosato, 1900 : LOCARD, (1905: 60). This name was never published by Monterosato. The authorship is to ascribe to Locard, 1905.
- *globosa*, *Bulla* as of Monterosato, 1902 MS. : LOCARD (1905: 43). The latter author himself noticed that the name was introduced by JEFFREYS (1867: 438) as *Bulla hydatis* var. *globosa*. Therefore the latter is the actual author of the name, raised to specific rank by LOCARD (1905).
- *membranacea*, *Philine* [or *Laona*] as of Monterosato MS. or Monterosato, 1880. Some authors – i.e. NORDSIECK (1972: 21), GAGLINI (1991: 12) – quoted this name followed by that of the Sicilian malacologist, although usually noticing that in his works it is simply a nomen nudum. This is right because *Philine membranacea* appears in MONTEROSATO (1880: 78 \562\) only, without any description or indication. In fact the name was made available by SYKES (1905: 324, fig. 2) by means of a drawing of the shell, an indication in the



Figs. 73-75: *Philine striatula*; Figs. 73a-c: syntype, Palermo, unrecorded depth, shell, shell top, and detail of sculpture on the central part of the body whorl; Figs. 74a-b: Vibo Marina, mud 300 m, shell and shell top (R. Ardovini legit; RV coll.); Figs. 75a-b: syntype, Cape San Vito, unrecorded depth (h: 3.5 mm). **Figs.** 76a-c: *Peracle diversa*, syntype of *Spirialis diversa*, Palermo, 210-280 m, shell, detail of sculpture, and shell top. **Scale bars:** 500 µm (73a, 74a), 200 µm (73b; 76a); 100 µm (73c, 74b, 76c); 20 µm (76b).

sense of the ICZN (1999: Art. 12.2.7). Thus the name should be quoted as: *Philine membranacea* Sykes, 1905, ex Monterosato MS.

- *obesiuscula*, *Cylichna* as of Monterosato, 1878 : Locard (1897: 71; 1905: 56) and Bouchet (1975: 334) ascribed this species to the Marquis, who never published this name, actually introduced by Brugnone (1877: 39-40; pl. 1, fig. 7). This name is present in the Monterosato coll. as a nomen in schedis. The labels show that Monterosato considered this species a full valid one, still not described. Later on, probably noticing the description by Brugnone, he employed the name *C. obesiuscula*, reporting also the opinion by Jef-

freys, who considered the species as distinct from *Cylichna ovata* Jeffreys in W.B. Carpenter & Jeffreys, 1871 (however cf. TRINGALI & OLIVERIO, 2001, this Volume, about its synonymy with *Pyrunculus ovatus*).

- *pyriformis* [or *piriformis*], *Retusa (Coleophysis)* as of Monterosato 1878 : NORDSIECK (1972: 34; 237, fig. 7), SETTEPASSI et al. (1976: 26), GROSSU (1986: 431; ibidem fig. 200), and KOUTSOUBAS & KOUKOURAS (1993: 193). *Utriculus truncatulus* var. "*piriformis*" [sic] by MONTEROSATO (1878a: 110 \424\; 1884: 142 \798\) is a nomen nudum. Therefore the author of the name is actually NORDSIECK (1972). Anyway the material labelled *Utriculus truncatulus* var. "*piriformis*"by Monterosato (ZMR) seems to match quite closely the drawing and description by NORDSIECK (1972) and it is likely that the German malacologist had examined it during a visit to the ZMR. It is difficult to judge whether this very slender form related to *Retusa truncatula*, with its sinuous outline and wide diameter of the top, is a distinct species, or a simple form of *truncatula*, as we provisionally regard it.

- *subquadrata*, *Bulla* as of Monterosato, 1902 MS. : LOCARD (1905: 43). The authorship of this taxon never published by Monterosato is in fact by Locard, 1905.

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Two new species of *Thorunna* Bergh 1878 (Mollusca: Nudibranchia: Chromodorididae) from the Indo-Pacific

Rebecca F. Johnson & Terrence M. Gosliner

KEY WORDS: *Thorunna*, Chromodorididae, Nudibranchia, Mollusca, Indo- Pacific, new species.

ABSTRACT The genus *Thorunna* previously included eleven described species. Two new species from the Indo-Pacific tropics, *Thorunna kahuna* and *Thorunna halourga* are described. *Thorunna kahuna* is the only known species in the genus with both large, visible mantle glands and small glands covering the dorsal surface. It also has a conical penial papilla inside a round penial bulb. This species is sympatric with a similarly colored species in the same genus, *Thorunna daniellae* (Kay & Young 1969). The other new species, *Thorunna halourga* is the only *Thorunna* known to have calcium carbonate spicules visible through the mantle surface.

RIASSUNTO A tutt'oggi il genere *Thorunna* include 11 specie. Due nuove specie dell'indo-pacifico tropicale, *Thorunna kahuna* e *T. halourga*, vengono qui descritte. *T. kahuna* è la sola specie del genere che presenti sia grandi che piccole ghiandole sulla superficie dorsale. Presenta inoltre una papilla peniale conica, all'interno di un bulbo arrotondato. Questa specie è simpatrica con *Thorunna daniellae* (Kay & Young, 1969), dalla colorazione simile. L'altra nuova specie, *T. halourga*, è l'unica specie del genere a possedere spicole di carbonato di calcio visibili attraverso la superficie del mantello.

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INTRODUCTION

The genus *Thorunna* (Bergh, 1878) is the most derived group in the family Chromodorididae (Gosliner & Johnson, 1999). All species in the genus are very small, less than 20 mm, have an extremely reduced labial armature and most species have lost the large, visible, defensive mantle glands found in all other chromodorid genera. Due to the loss or reduction of many structures traditionally used for classification of nudibranchs in the family Chromodorididae, some species of *Thorunna* have been separated using biogeography and slight differences in their external coloration (see Rudman, 1984). The strength of these distinctions would be substantially increased by the utilization of new characters. A number of previously uninvestigated characters are examined here. They include small, dorsal mantle glands, buccal bulb glands, and two structures found in the male portion of the reproductive system.

SPECIES DESCRIPTIONS

Thorunna kahuna sp.nov.
(Figures 1A, 2-5)

Babaina daniellae Bertsch & Johnson, 1981:109; not (Kay & Young, 1969)
Thorunna sp. Hoover, 1998:169 lower photograph

Type material

Holotype: CASIZ 087069, dissected, Aino Moana State Park, Mamala Bay, Magic Island, Honolulu, Oahu Island, Hawaii, 6 m depth, 8 February 1986, T.M. Gosliner.

Etymology

The name *Thorunna kahuna* comes from the Hawaiian word for medicine man or healer. Unlike most members of the genus *Thorunna*, *T. kahuna*, has visible mantle glands. These glands contain toxic chemicals and are thought to deter predation. In hopes of finding novel chemicals that may aid in the treatment of disease biochemists have begun to analyze chemicals isolated from the mantle glands of other chromodorid nudibranchs (Avila, 1995). Eventually, *T. kahuna* and other chromodorids may serve as modern day kahunas.

Distribution

The only known records of *Thorunna kahuna* are from the waters off Magic Island just off the coast of Honolulu on Oahu Island, Hawaii. This single specimen was found, and others have been observed, at up to 6m depth.

External morphology

The living animal was 12 mm in length (Fig. 1A). The body is oval and elongate. The mantle is slightly laterally constricted in the area adjacent to the gills. Posterior to this narrow portion, the mantle again widens and thickens. The mantle is white with a slight pinkish tinge. The body is opaque in the center and becomes more translucent along the mantle edge. The foot is the same color as the mantle, with a thin pink border around the edge of the foot. There is a sub-marginal, dashed, magenta line around the mantle. The magenta areas may be broken up further into small dots. A single row of opaque white mantle glands is visible through the translucent white mantle edge. There are 10-12 glands concentrated in the posterior region of the mantle, and one or two glands are visible on either

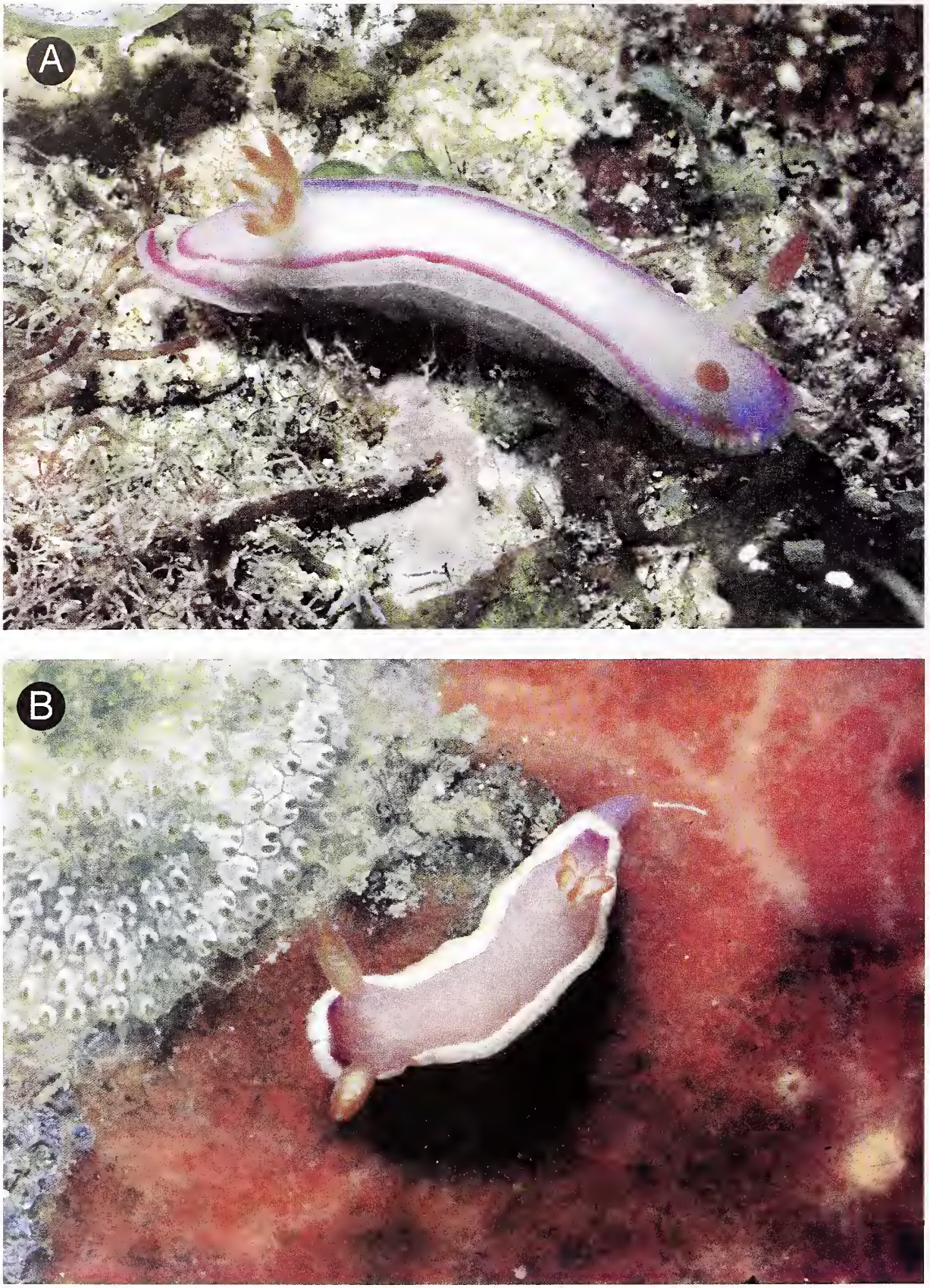

Figure 1. Living animals. A. *Thorunna kahuna* **sp. nov.** CASIZ 087069, 12 mm in length, Magic Island, Honolulu, Hawaii. B. *Thorunna halourga* **sp. nov.** CASIZ 086434, 10 mm in length, Rasch Passage, Madang, Papua New Guinea.

side of the head. The mantle overhang is also covered with minute, raised glands. These glands are arranged in concentric rings around the mantle and are barely visible without a dissection microscope (Fig. 2). The simple gills are white at the base and reddish-orange at the tips. The rhinophores are very long and club-like. They are pinkish-white at their bases and reddish-orange at the apexes.

Alimentary canal

The oral tube is twice as long as the muscular portion of the buccal mass. There is a wide ring of glandular tissue surrounding the oral tube (Fig. 3). The radular formula is 34 x 18.0.18 . There is no differentiation between the inner lateral teeth and all of the other teeth. It is difficult to determine whether the teeth have a primary cusp with denticles or many cusps. They will be called denticles for ease of discussion. There are 5-9 denticles on each tooth. One or two denticles are turned toward the center of the radula, whereas the remainder of the denticles are pointed toward the outer edges of the radula (Fig. 4A). On most teeth, the last denticle on the outer edge of the tooth is much more pointed than the rest of the denticles. The bases of the teeth are flattened and greatly elongated (Fig. 4B, C). The jaws are small and delicate. They are composed of bifid or multifid elements. These small thin rodlets join together to form single recurved hooks (Fig. 4D).

Reproductive system

The arrangement of organs is triaulic (Fig. 5). The ampulla is short and irregularly rounded. It tapers into a thin, muscular tube before it joins with the prostate and enters the female gland mass. The prostate is wide and highly convoluted, but narrows into the ejaculatory portion. The ejaculatory portion is very short and narrow, but muscular. It widens into a very large round, muscular bulb at the top of the penis. A small, conical papilla is visible through the musculature of this bulb. The penis is very long and narrow. The bursa copulatrix is large and rounded. The large, elongate, pyriform receptaculum seminis bends sharply at the point where it enters the bursa copulatrix. The common uterine and vaginal duct enters the bursa copulatrix at this point, as well. This long, thin duct divides into the uterine duct and the vaginal duct close to the female gland mass. The short and narrow uterine duct continues into the female gland mass, whereas the vaginal duct widens slightly and meets the penis to form the common genital opening. A thin, highly ramified vestibular gland surrounds the entire female side of the reproductive system and is attached to the base of the female gland mass.

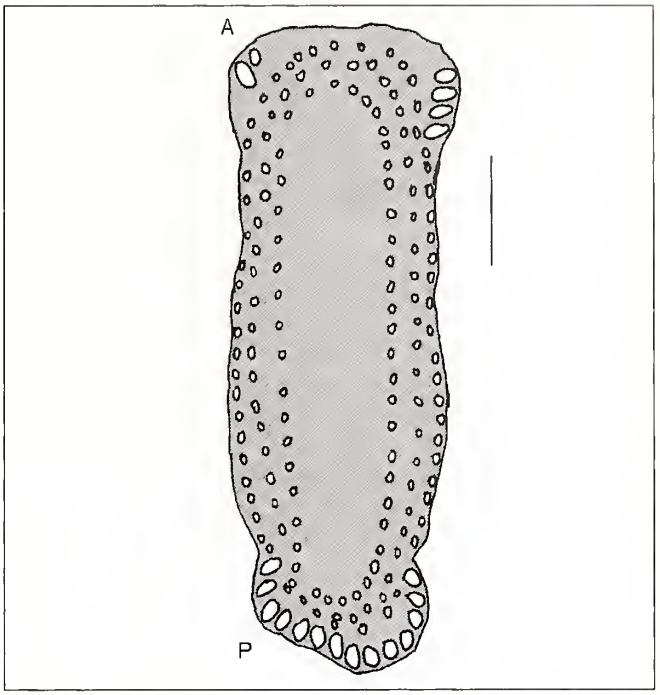

Figure 2. Mantle glands. *Thorunna kahuna* sp. nov. Abbreviations: A- anterior, P- posterior, dorsal side faces up. Scale = 2mm.

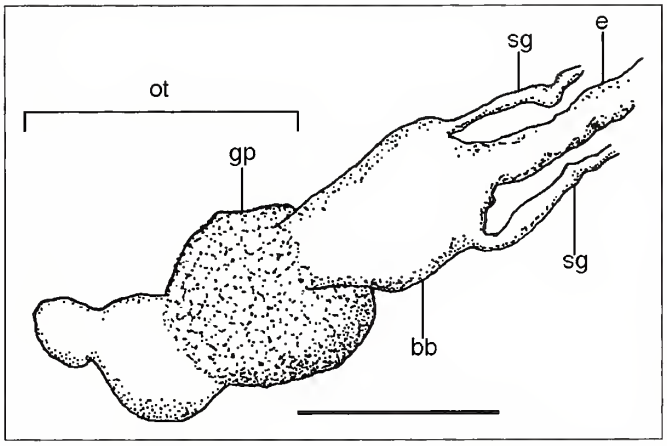

Figure 3. Alimentary canal. *Thorunna kahuna* sp. nov. Abbreviations: bb- buccal bulb, e- esophagus, gp- glandular portion, ot- oral tube, sg- salivary gland. Scale bar = 1 mm.

DISCUSSION

Thorunna kahuna is most similar in external morphology to *T. daniellae*. They are both whitish in color with a purple to pink mantle border. *Thorunna daniellae* has a much more opaque white general body color that becomes translucent on the outside of the maroon mantle margin and has distinct translucent patches behind and around the rhinophores (Hoover, 1998), whereas *T. kahuna* is a uniform pinkish white all over the mantle except for the pinkish maroon mantle border. *Thorunna kahuna* has white rhinophoral stalks and orangish- red rhinophore clubs. *Thorunna daniellae* has translucent rhinophoral stalks and its rhinophore clubs are reddish on the anterior side and opaque white on the posterior facing side. The gills are similar, but *T. kahuna* has uniformly orangish-red gills with translucent white bases and *T. daniellae* has opaque white gills with orangish-red rachises. The most distinct external difference between these species is the presence of large, visible mantle glands on the sides of the head anterior to the rhinophores and posterior to the gills in *T. kahuna* (Fig. 2, Bertsch & Johnson, 1981:109). Visible mantle glands are not

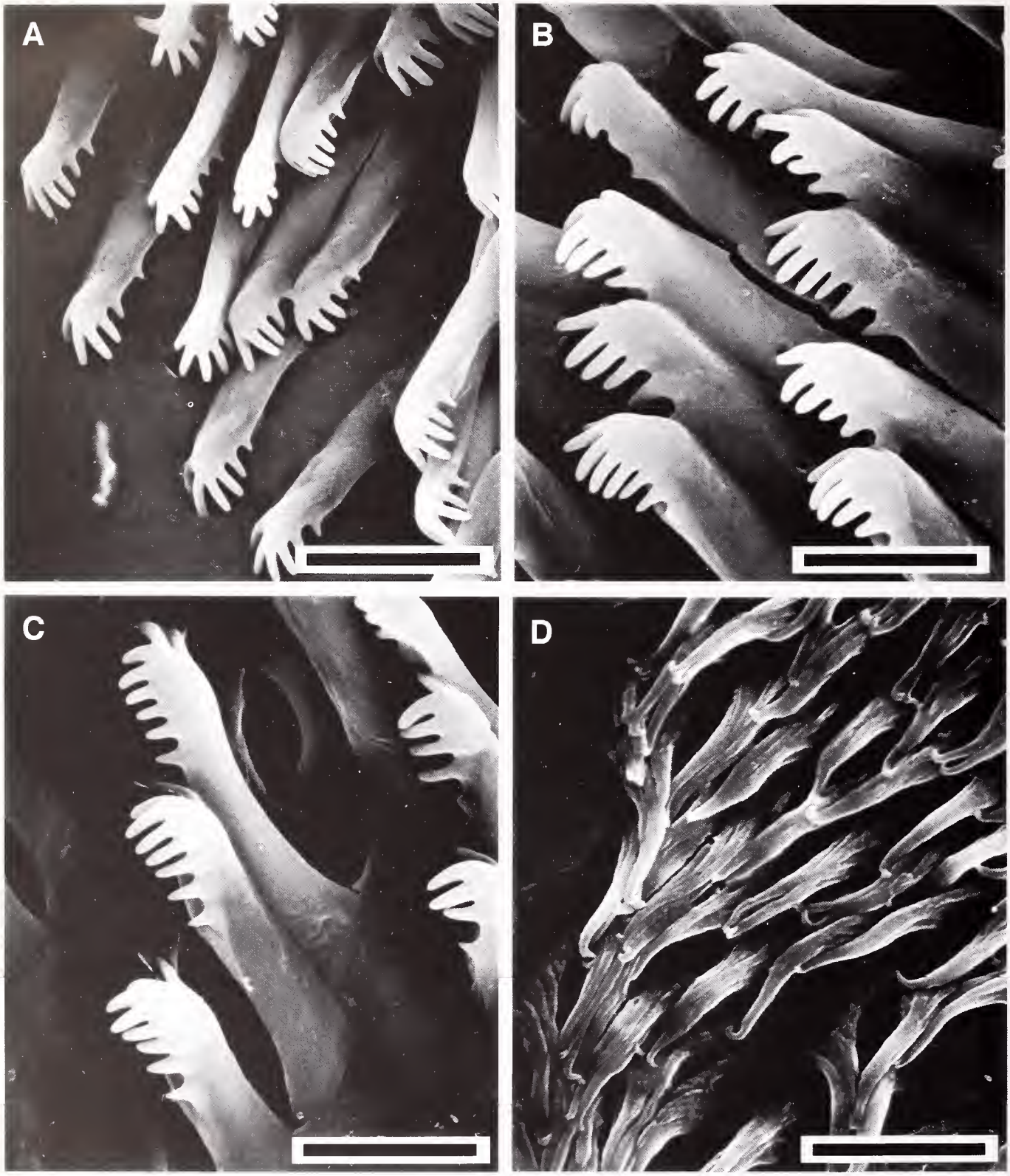

Figure 4. Scanning electron micrographs. *Thorunna kahuna* sp. nov. CASIZ 087069. A. Inner lateral teeth. Scale = 15 µm. B. Middle lateral teeth. Scale = 10 µm. C. Outer lateral teeth. Scale = 10 µm. D. Jaw rodlets. Scale = 15 µm.

present in *T. daniellae* (KAY & YOUNG, 1969; RUDMAN, 1984), although, a row of tiny glands visible only with a scanning electron microscope has been found on the notum of *T. daniellae*. These glands may be similar to the minute dorsal glands found in *T. kahuna*, except that *T. kahuna* has multiple, concentric rings of glands on the dorsal surface, and *T. daniellae* only has one sub-marginal row. This type of dorsal gland has never been reported for any member of the family Chromodorididae. Further investigation is needed to determine if this type of dorsal gland arrangement is present in other chromodorids.

The radular morphology of these two species is very different. *Thorunna kahuna* has multiple cusps (5-7) on each tooth and all of the teeth are the same general shape, there is no differentiation between the inner and outer lateral teeth. *Thorunna daniellae* has bifid middle and outer laterals and short multifid inner lateral teeth (RUDMAN, 1984). The jaw morphology is very similar in the two species. *Thorunna daniellae* lacks the large penial bulb and conical papillae found in *T. kahuna*. The vaginal duct and the uterine duct in *T. daniellae* branch at a point that is closer to the bursa copulatrix than the branching point in *T. kahuna*. *Thorunna kahuna* also has a wider penis than *T. daniellae*.

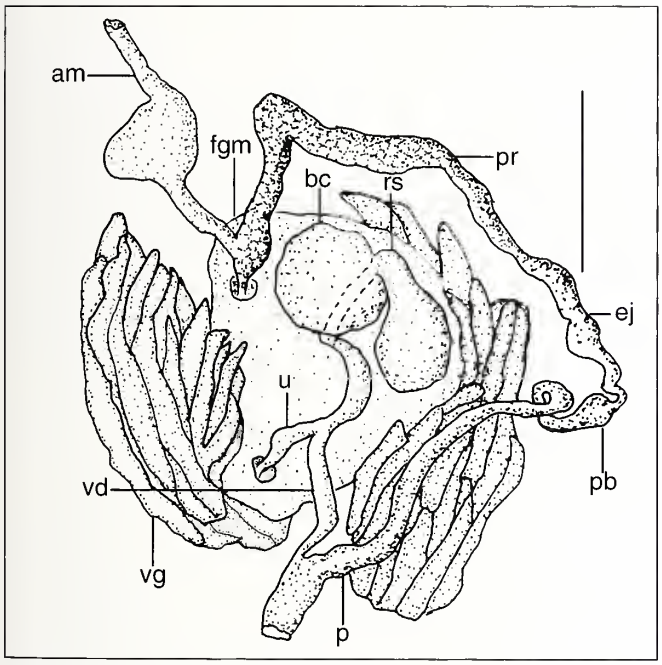

Figure 5. Reproductive system. *Thorunna kahuna* sp. nov. CASIZ 087069. Abbreviations: am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of the vas deferns, fgm- female gland mass, p- penis, pb- penial bulb, pr- prostate, rs- receptaculum seminis, u- uterine duct, vd- vaginal duct, vg- vestibular gland. Scale = 1mm.

Thorunna halourga sp.nov.
(Figures 1B, 6-8)

Type material

Holotype: CASIZ 075089, Rasch Passage, Madang, Papua New Guinea, 9 m depth, 17 November 1990, T.M. Gosliner and G. Williams.

Paratypes:

CASIZ 1103605, one specimen, dissected, Basilisk Point, Milne Bay Province, Papua New Guinea, 3 m depth, 28 May 1988, T.M. Gosliner.

CASIZ 075265, three specimens, Planet Rock, south of Madang, Papua New Guinea, 44 m depth, 21 November 1990 T.M. Gosliner, G. Williams and M. Jebb.

CASIZ 086434, one specimen, Rasch Passage, Madang, Papua New Guinea, 50 m depth, 9 June 1992, T.M. Gosliner.

CASIZ 086321, two specimens, south side of Rasch Passage, Madang, Papua New Guinea, 5 m depth, 16 June 1992, T.M. Gosliner.

CASIZ 110452, two specimens, Bethlehem, Maricaban Island, Batangas Province, Luzon Island, Philippines, 24 April 1997, T.M. Gosliner.

Etymology

The name *Thorunna halourga* comes from the Greek word halourgus, which means sea-purple. The body color of this tiny animal is a brilliant purple.

Distribution

This animal has been found only in Papua New Guinea and the Batangas region of the Philippines. *Thorunna halourga* has been observed at depths from 3 to 50 meters.

External morphology

The living animal is 10 mm in length (Fig. 1B). The body color ranges from a light purplish-pink to a deep purple. This purplish color is darker at the posterior and anterior ends of the animal, where a thick white mantle margin begins. The mantle margin is slightly undulate and opaque, but may become more translucent at the edges. The foot is darker in color than the rest of the body. The rhinophores and gills range from a light almost white to orange or dark red. In the darker animals, the rhinophores and gills are darker as well. The rhinophores are translucent at the bases and dark reddish at the tips. The color pattern of the area in between the translucent and reddish portion is highly variable. On the rhinophores of some specimens there is a purple band present and in others a white band, and some have both bands. There is no evidence of mantle glands anywhere on the animal, but miniscule glands may be present around the mantle margin. Arranged in a chevron-like pattern, on the dorsum, there are spaces where calcium carbonate spicules were present (Fig. 6). Calcium carbonate structures are often lost after the fixation of the specimens in Bouin's solution. The spicules are visible in the living animals (Fig. 1).

Alimentary canal

The oral tube is twice as long as the muscular portion of the buccal mass. There are no glandular structures present on the oral tube or buccal bulb. The radular formula is 38 x 27-29.0.27-29. The inner lateral radular teeth have very wide bases, but narrow into thin, curved cusps (Fig. 7A). The inner 2-3 teeth are bifid, but the second cusp is much smaller and

more pointed than the first. The rest of the middle and outer lateral teeth are long, have wide bases and have cusps that are equal in length (Fig 7B, C). The jaws are extremely small and delicate (Fig. 7D). They are long and thin. Most rodlets share a common base with other rodlets, but then separate into individual, pointed, re-curved hooks.

Reproductive system

The arrangement of organs is triaulic (Fig. 8). The ampulla is short and rounded. It tapers into a thin, muscular tube before it joins with the prostate and enters the female gland mass. The ampulla narrows and lengthens toward its distal end. The glandular portion of the prostate forms a simple loop that narrows into the ejaculatory portion. The ejaculatory portion is short and thin, but muscular. It widens into a round, muscular bulb at the top of the penis. The penis is very long and narrow. The bursa copulatrix is large and rounded. The large, elongate, pyriform, receptaculum curves slightly at the point where it enters the bursa copulatrix. The common uterine and vaginal duct enters the bursa copulatrix at this point, as well. This long, thin duct divides into the uterine duct and the vaginal duct close to the female gland mass. The short and narrow uterine duct continues into the female gland mass, whereas the long vaginal duct widens slightly and meets the penis to form the common genital opening. A thin, highly ramified vestibular gland surrounds the entire female side of the reproductive system and is attached at the base of the female gland mass.

DISCUSSION

Thorunna halourga is the only member of the genus *Thorunna* with a purple mantle and a wide, white mantle border. It is most similar to *Thorunna punicea* (RUDMAN, 1995), but *T. punicea* is lighter in color, has a fairly narrow mantle border and purple tipped rhinophores and gills. *Thorunna halourga* and *T. punicea* have similar color patterns and reproductive systems and both lack mantle glands, but their radulae are quite different. *Thorunna halourga* has a relatively narrow radula, 38x 27-29.0.27-29, while *T. punicea* has a wider radula, 38x 36.0.36.

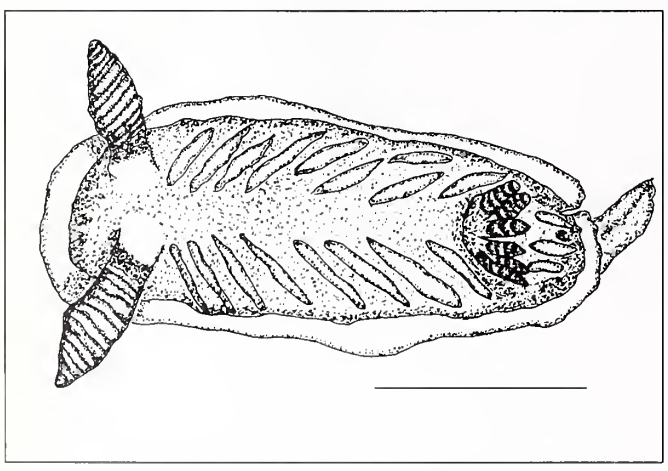

Figure 6. Mantle spicules. *Thorunna halourga* sp. nov. CASIZ 075265. Abbreviation: s- spicules. Scale = 2mm.

The teeth of *T. punicea* are much larger and more developed than those of *T. halourga*. The inner tooth in *T. punicea* has a small denticle on the inside of the bifid cusp, while *T. halourga* lacks an inner denticle and has one greatly reduced cusp. The teeth *of T. halourga* are also much thinner and longer than those of *T. punicea*. The outermost teeth of *T. punicea* have a number of outer denticles, whereas *T. halourga* lacks any outer denticles on any teeth. The jaw rodlets of *T. punicea* are wide, flat and much more developed than the thin long rodlets of *T. halourga*. In the description of *T. punicea* there is no mention of calcium carbonate spicules in the mantle, but these spicules could have easily been overlooked and may have dissolved due to preservation, as mentioned above.

Thorunna halourga is similar in color pattern to all of the animals included in Rudman's (1986) "*Noumea purpurea* colour group". These include *Noumea purpurea*, *Noumea varians*, *Pectenodoris trilineata*, *Durvilledoris similaris* and *Durvilledoris pusilla*. All of these species have a pinkish purple background color and a white or yellowish mantle border. Unlike all of these species, which all have other white or yellow lines on their mantle surfaces, *T. halourga* does not have any markings on its mantle surface other than the mantle border. *Thorunna halourga* is similar to all of the aforementioned species in external coloration only, their internal anatomies are very different. All five of the species in this color group have visible mantle glands, whereas *T. halour*ga does not have any mantle glands. The radula of *T. halourga* is almost as wide as it is long , is greatly reduced and very thin and delicate. Its radular formula is 38x 27-29.0.27-29, as mentioned above. *Noumea purpurea*, *N. varians*, *Durvilledoris similaris* and *D. pusilla* all have extremely narrow radulae with greatly enlarged inner-most teeth and multiple denticles on the other lateral teeth. Their radular formulas are 28x 14.0.14, 39x 18.0.18, 23x 11.0.11and 44x 19.0.19 respectively. *Pectenodoris trilineata* (JOHNSON & GOSLINER, 1998) has very distinct, extremely short radular teeth. These teeth differ greatly from the long narrow teeth of *T. halourga*. All of the species in the *Noumea purpurea* color group have similar reproductive systems. In all of these species the receptaculum seminis enters directly into the bursa copulatrix. The arrangement of the reproductive system of *T. halourga* is very similar to that of the members of this color group, except the ampulla in *T. halourga* is more rounded than in the other species.

Thorunna halourga is also similar in color to *Durvilledoris albofimbria* (RUDMAN, 1995). *Durvilledoris albofimbria* is purplish-pink in color with a thin white mantle margin, unlike the wide white mantle margin found in *T. halourga*. *Durvilledoris albofimbria* differs from both *T. halourga* and *T. punicea* in that it has large visible mantle glands around the entire mantle edge. Visible mantle glands are not found in either of these species of *Thorunna*. *Durvilledoris albofimbria* also differs from *T. halourga* in its internal morphology. The radular formula of *D. albofimbria* is 35x18.0.18, similar, but more narrow than that of *T. halourga* (see above). The biggest radular difference is that *D. albofimbria* has a tricuspid inner tooth, whereas *T. halourga* has a simply bifid inner lateral tooth. *D. albofimbria* may also have slightly larger jaw rodlets than *T. halourga*. The biggest inter-

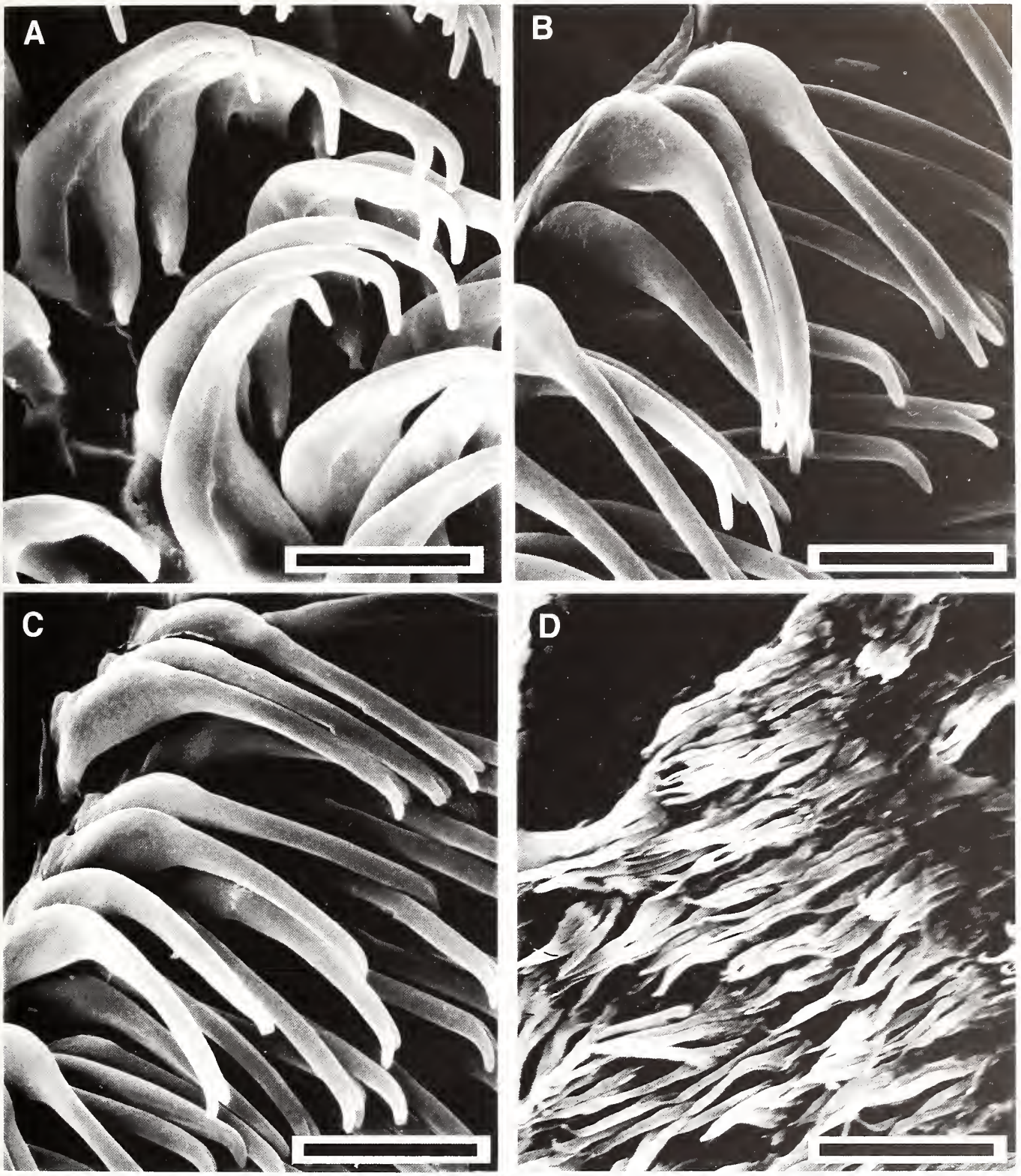

Figure 7. Scanning electron micrographs. *Thorunna halourga* **sp. nov.** CASIZ 113605. A. Inner lateral teeth. Scale = 15 µm. B. Middle lateral teeth. Scale = 15 µm. C. Outer lateral teeth. Scale = 20 µm. D. Jaw rodlets. Scale = 15 µm.

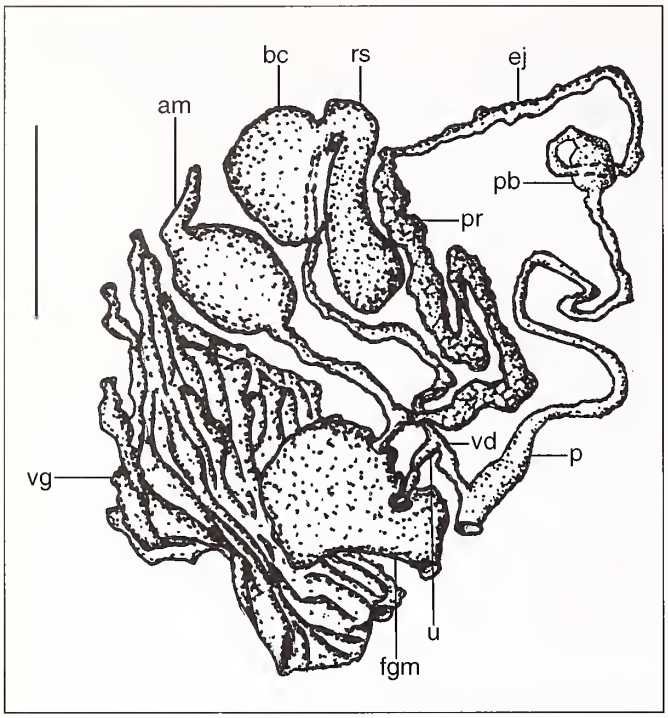

Figure 8. Reproductive system. *Thorunna halourga* sp. nov. CASIZ 113605. Abbreviations: am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of the vas deferns, fgm- female gland mass, p- penis, pb- penial bulb, pr- prostate, rs- receptaculum seminis, u- uterine duct, vd- vaginal duct, vg- vestibular gland. Scale = 1mm.

nal difference between these two species is the receptaculum seminis. *Durvilledoris albofimbria* has a minute receptaculum seminis, as described for all Indo-Pacific *Hypselodoris* (GOSLINER & JOHNSON, 1999), attached to the vaginal duct at the base of the bursa copulatrix, and *T. halourga* has a large receptaculum seminis, connected directly to the bursa copulatrix. *Durvilledoris albofimbria* also has a much shorter more muscular penis and a long, narrow ampulla.

ACKNOWLEDGEMENTS

Hans Bertsch, Scott Johnson, and Cory Pittman kindly provided specimens and data for the species studied here. Field work was supported by Katharine Stewart, The Christensen Research Institute, the In-house Research fund of the California Academy of Sciences and United Airlines. Support was also provided by the Graduate Assistantship Program of the California Academy of Sciences. Dong Lin printed the final electron micrographs.

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The Recent Mediterranean species of the genus *Pyrunculus* Pilsbry, 1895 (Opisthobranchia, Cephalaspidea, Retusidae)

Lionello P. Tringali & Marco Oliverio

KEY WORDS: Retusidae; *Pyrunculus*; systematics; morphology; North-eastern Atlantic; Mediterranean; marine; Recent.

ABSTRACT The present work is an attempt to update the check-list of the Mediterranean species of *Pyrunculus* Pilsbry, 1895. The species have been ascribed to the genus on the base of: (a) the small sized bubble-shell, characteristically peat-shaped; (b) the gizzard plates (three), subtriangular in shape, corneous, light brown colouted, with two darker blunt tubercles. Three members of the genus are considered as present in the Mediterranean Sea: *Pyrunculus ovatus* (Jeffreys *in* W.B. Carpenter & Jeffreys, 1871), *P. hoernesii* (Weinkauff, 1866), and *P. fourierii* (Audouin, 1827). *P. ovatus* is still living in the Atlantic, but is possibly extinct in the Mediterranean waters. *Cylichna obesiuscula* Brugnone, 1877, is regarded as a form of *P. ovatus*, as probably is also *Cylichna obscura* Sykes, 1904. The view of TRINGALI (1993) that *Cylichna hoernesii* Weinkauff, 1866, should be assigned to *Pyrunculus* is confirmed. *Cylichna cuneata* Tiberi, 1868, is a synonym of *P. hoernesii*. *Bulla fourierii* Audouin, 1827, usually included in *Retusa*, is assigned to *Pyrunculus* basing on its gizzard plates. The shell morphology itself does not allow to give this systematic position. The species is a Lessepsian migrant, apparently well-acclimatised in the Levant Sea, and widespread through the Indo-Pacific waters. There are other more recent names possibly available for *P. fourierii*: *Bulla decussata* A. Adams, 1850, *Utriculus simillimus* R.B. Watson, 1883, *Cylichna protumida* Hedley, 1903, all to be checked on the type material. The statement by BOGI & KHAIRALLAH (1987) that the Tunisian *Retusa dilatata* Pallary, 1904, and its variety *minor* Pallary, 1904, are synonyms of *P. fourierii*, is rebutted. *Utriculus minutissimus* Monterosato, 1878, considered by several workers as a *Pyrunculus*, must be removed from this genus, being a *Retusa*, as shown by both the shell and the gizzard plates morphology.

RIASSUNTO Questo lavoro presenta un tentativo di aggiornamento della lista delle specie mediterranee appartenenti al genere *Pyrunculus* Pilsbry, 1895. Le specie sono state attribuite al genere tenendo conto di due caratteristiche: (a) la piccola conchiglia bulliforme e tipicamente piriforme; (b) le tre piastre gastriche – situate in un'espansione dell'esofago che potrebbe essere chiamata, più specificamente, ventriglio (ingl. "gizzard"), per analogia con l'organo degli uccelli, funzionale al trattenere e frantumare i nicchi calcarei delle prede (foraminiferi per le specie di *Pyrunculus*) - subtriangolari, cornee, di colore bruno chiaro, con due soli noduli, di colore bruno scuro. Le piastre gastriche del genere *Retusa* T. Brown, 1827, assai prossimo, sono simili, ma presentano numerosi noduli sulla superficie, e di minori dimensioni. Tre specie vengono qui considerate presenti in Mediterraneo: *Pyrunculus ovatus* (Jeffreys in W.B. Carpenter & Jeffreys, 1871), *P. hoernesii* (Weinkauff, 1866), and *P. fourierii* (Audouin, 1827). Non è ancora chiaro se il primo sia reperibile in Mediterraneo soltanto come fossile pleistocenico, mentre è certamente vivente in Atlantico. *Cylichna obesiuscula* Brugnone, 1877, è considerata una forma di *P. ovatus*, così com'è assai probabilmente anche *Cylichna obscura* Sykes, 1904. Viene confermata l'attribuzione a *Pyrunculus* di *Cylichna hoernesii* Weinkauff, 1866, proposta da TRINGALI (1993). *Cylichna cuneata* Tiberi, 1868, è un sinonimo. *Bulla fourierii* Audouin, 1827, in genere attribuita a *Retusa*, è da spostare in *Pyrunculus*, in base alle piastre gastriche. Va rilevato come la morfologia conchiliare della specie non suggerisca, per se stessa, l'attribuzione a questo genere. *P. fourierii* è un immigrante lessepsiano, largamente diffuso nell'Indo-Pacifico, avendo a disposizione anche altri nomi - *Bulla decussata* A. Adams, 1850, *Utriculus simillimus* R.B. Watson, 1883, *Cylichna protumida* Hedley, 1903, tutti, però, da verificare definitivamente sul materiale tipico. Contrariamente a quanto indicato da BOGI & KHAIRALLAH (1987), la tunisina *Retusa dilatata* Pallary, 1904, e la sua varietà *minor* Pallary, 1904, non sono sinonimi di *P. fourierii*, ma piuttosto entità correlate a *Retusa truncatula* (Bruguière, 1792), forse semplici forme giganti di quest'ultima, con altezza fino a 7 mm circa. La presenza di *P. fourierii* in Mediterraneo, perciò, sembra limitata al bacino di Levante, non raggiungendo le acque della Tunisia. *Utriculus minutissimus* Monterosato, 1878, considerato da vari autori quale membro di *Pyrunculus*, deve essere rimosso da questo genere, essendo una *Retusa*, come mostra la morfologia conchiliare, e conferma la forma delle piastre gastriche.

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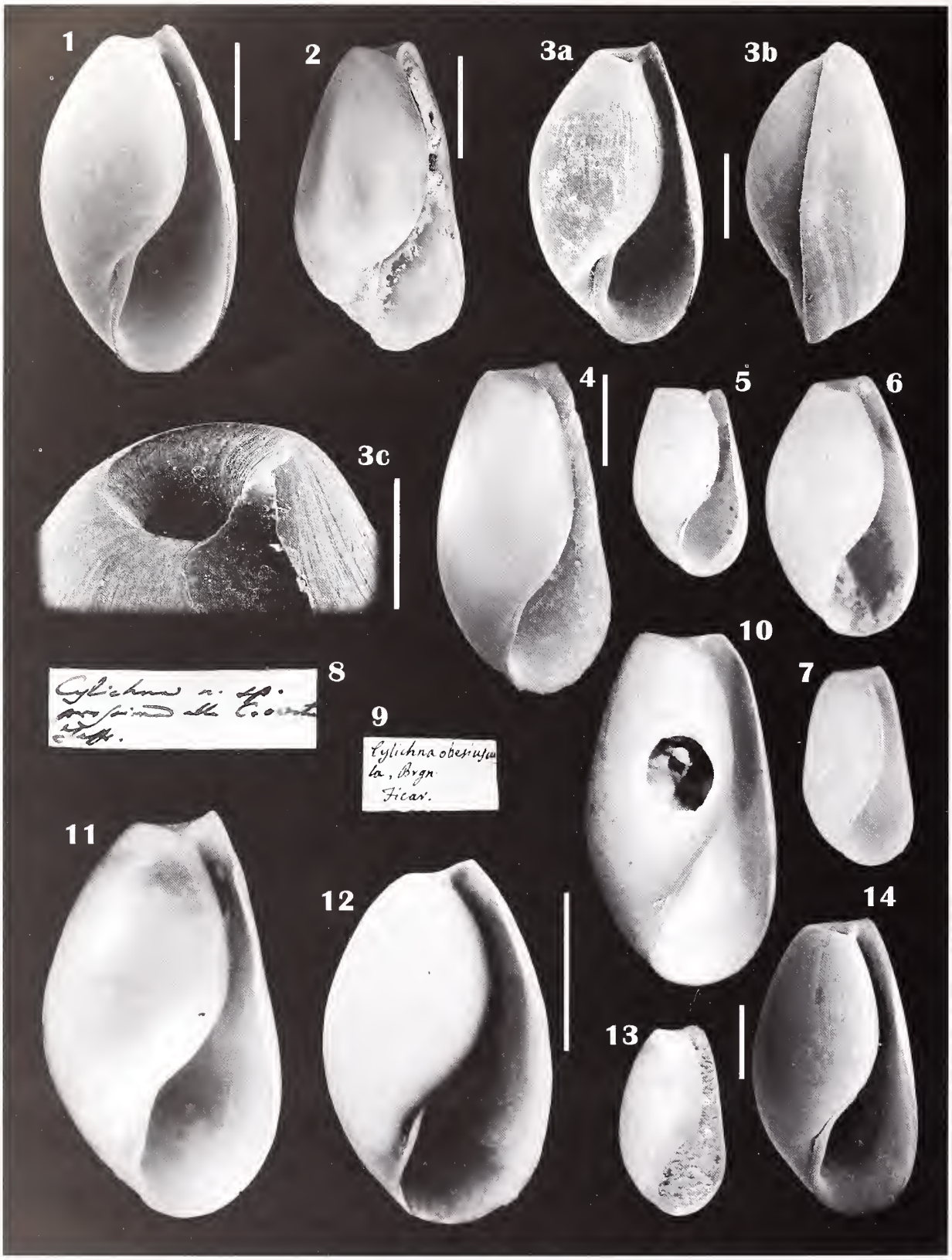
INTRODUCTION

The Eastern Atlantic and Mediterranean gastropods belonging to the order Cephalaspidea P. Fischer, 1883 [= Bullomorpha Pelseneer, 1906], have obtained little attention by malacological research, thus their systematics and nomenclature are poorly known.

The aim of the present report is to update the check-list of the Mediterranean species of the genus *Pyrunculus* Pilsbry, 1895. We nevertheless advise the readers not to regard this as a full systematic review of such a scarcely known group of species. The data available to us are still rather scanty, based on hard parts only, i.e. shell and gizzard plates. Moreover several questions remain still unanswered. Our provisional conclusions are, however, somewhat diverging from those proposed by the other lists of Mediterranean species of the genus, with emendatio, addenda, changes of systematic position and newly proposed synonymies.

Abbreviations and acronyms

AMS: Australian Museum, Sydney, Australia;
coll./colls.: collection/collections;
frg./frgs.: shell fragment/fragments;
leg.: collected by (after Latin: "legit");
LPT: Lionello Paolo Tringali, Rome;
MNHN: Museum National d'Historie Naturelle, Paris, France;
MO: Marco Oliverio, Dip. Biologia Animale e dell'Uomo, "La Sapienza" Roma-I University, Rome;
NHML: Natural History Museum, London, U.K.
sh./shs.: specimen/specimens collected without soft parts;
spm./spms.: specimen/specimens collected with the soft parts;
USNM: United States National Museum, Smithsonian Institution, Washington, U.S.A.
ZMR: (Township) Zoological Museum, Rome, ("Museo Civico di Zoologia, Roma"), Italy.



Figs. 1-14. *Pyrunculus ovatus* (Jeffreys) - **Figs. 1, 2, 3a-c**: syntypes of *Cylichna obesiuscula* Brugnone, Ficarazzi (Palermo, Sicily) (Monterosato coll.); **Figs. 4-7**: "Princesse Alice" exp. (1895), Stn. 46, 1385 m (Monterosato coll.) (Figs. 5, 6, 7 respective h: 3.3, 3.0, 3.6, 2.9 mm); **Fig. 8**: original label by Monterosato noticing that the swollen form would be a new species, similar to *P. ovatus*; **Fig. 9**: original label of *Cylichna obesiuscula* by Brugnone; **Fig. 10**: "Triton" exp. (1881), Stn. 13, 555 fathoms (= 1026 m ca.), off North Great Britain (h: 3.2) (Monterosato coll.); **Fig. 11**: Mauritania, fishing net residue, 900-1200 m (h: 3.4 mm) (F. Gubbioli leg.); **Fig. 12**: "De Profundis" Project (1991 exp.), Stn. DP91-4, East Sardinia, 571-347 m; **Figs. 13-14**: "Talisman" exp. (1883), Stn. 127, Azores, between Pico and St. Georges, 1258 m (Monterosato coll.) (Fig. 13 h.: 3.1 mm) - **Scale bars**: 2.0 mm (2); 1.0 mm (1, 3a, 3b, 4, 12, 14); 400 µm (3c).

Some general remarks on *Pyrunculus*

Pyrunculus PILSBRY, 1895 (: 181, 229), was proposed as a new name to replace *Sao* H. Adams & A. Adams, 1854 [non Bilberg, 1820, nec Barrande, 1846, nec Kölliker, 1853], thus acquiring the same type species, namely the Chinese *Bulla pyriformis* A. Adams, 1850, by monotypy (ADAMS & ADAMS, 1854: 21). Adams brothers introduced *Sao* as a subgenus of *Atys* Montfort, 1810, whereas PILSBRY (1895: 181) provisionally regarded *Pyrunculus* as a subgenus of *Retusa* T. Brown, 1827. The position in the family Retusidae Thiele, 1931, is widely accepted nowadays.

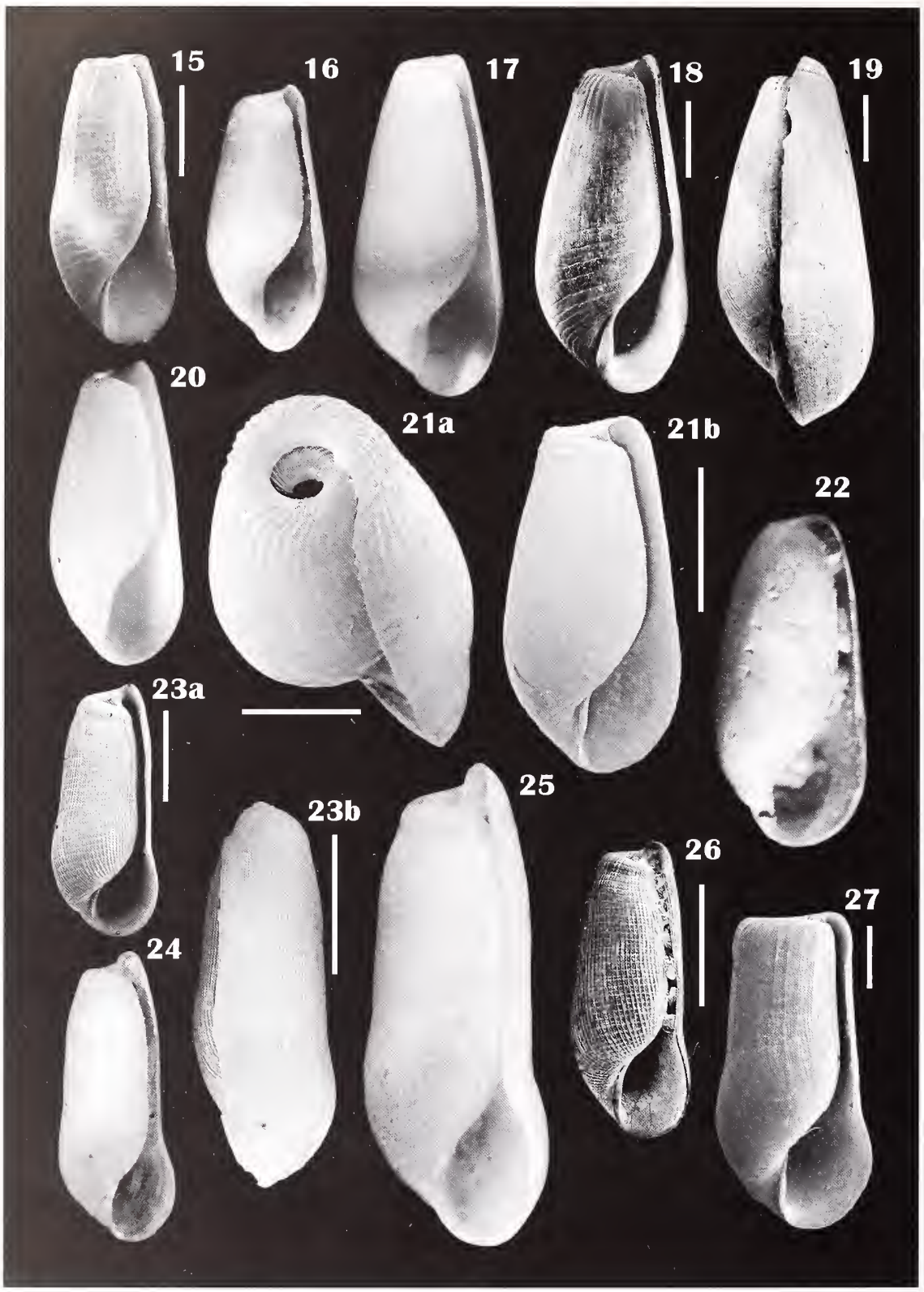
Sao pyriformis has a distinctly pear-shaped (= pyriform) shell, which gradually swells downward, and has a deeply sunken spire, barely visible through the apical umbilicus. For a long time *Sao/Pyrunculus* species were simply identified on account of the pear-shaped outline of the shell (PILSBRY, 1895: loc. cit.). In the twentieth century it became evident that the gizzard plates add a further feature to identify them (THIELE, 1931: 389; BOUCHET, 1975: 333). The anterior digestive tract of the members of *Pyrunculus* includes a gizzard with three small corneous plates, employed to enclose preys – as far as it is known, foraminifers - and/or to crush their tests. The plates are reminiscent of those of the genus *Retusa*, nearly triangular in shape, slightly curved, light brown coloured with darker tubercles; however each plate of *Pyrunculus* bears two tubercles only (Figs. 35-37) whereas on the plates of *Retusa* there are several smaller tubercles spread on the plates' surface. Data on the gizzard plates of some species of *Retusa* have been already gathered in literature since nineteenth century, e.g.: *Retusa truncatula* (Bruguière, 1792) (SARS, 1878: anatomical pl. XI, fig. 8; PILSBRY, 1895: pl. 60, fig. 4; VAYSSIÈRE, 1934: fig. 6; THOMPSON, 1976: 114; LUQUE, 1983: 54, fig. 2b; also personal observations on material from Southern Turkey and Mediterranean Morocco), *Retusa nitidula* (Lovén, 1846) (SARS, 1878: anatomical pl. XI, figs. 6a-b; PILSBRY, 1895: pl. 60, figs. 6-7), *Retusa sosa* MARCUS & MARCUS, 1969 (: 7; 5, fig. 7), *Retusa pelyx* Burn in BURN & BELL, 1974 (: 38; 39, fig. 4), *Retusa obtusa* (Montagu, 1803) (SARS, 1878: anatomical pl. XI, fig. 9, as «*Utriculus pertenuis* (Mighels, 1842)»; SMYTHE, 1979: 96-97; pl. IV, fig. 13; MIKKELSEN, 1996: 391, fig.30); *R. tarutana* SMYTHE, 1979 (: pl. 4, fig. 13); *Retusa umbilicata* (Montagu, 1803) (SARS, 1878: anatomical pl. XI, fig. 7; PILSBRY, 1895: pl. 60, fig. 8). Additionally we noticed the same gizzard plates morphology for *Retusa desgenettii* (Audouin, 1827) (Figs. 39a-b), *Retusa mamillata* (Philippi, 1836) (Figs. 38a-b) and *Retusa minutissima* (Monterosato, 1878) (see OLIVERIO & TRINGALI, 2001, this Volume: figs. 43a-b) after material from Sudan, Southern Turkey, and Southeast Spain, respectively. Traditionally *Pyrunculus* and *Retusa* have been regarded as closely related, a view we share, with *Pyrunculus* as a distinct genus within the same family, also considering other retusid genera – such as *Relichna* Rudman, 1971, – are regarded as distinct according to the gizzard plates morphology.

It is not always easy to recognise members of these genera on the basis of the shell morphology. A somewhat pear-shaped shell may be also found in some species of *Retusa*, albeit usually with a more marked recess just above the half of the height. Other shell features – sculpture, colour, shape of the top, etc. – do not seem unfailing as distinctive traits. *Pyrunculus* species lack a radula and jaws structures (e.g. BOUCHET, 1975: 332; MORENO & TEMPLADO, 1998: 48), as is typical of retusid gastropods, including *Retusa*. We had not access to properly fixed material of any species, yet fresh dead retusids may still keep the corneous plates even if the soft parts are reduced to few poor residues inside the shell. Thus, we have been able to examine and photograph the gizzard plates of all the species discussed in the following notes. Therefore, we have adopted as criteria to identify *Pyrunculus* species those traditionally accepted: (a) the shell morphology, with special attention to the pear-shaped outline; (b) the gizzard plates morphology, considering this latter as a decisive character. Shells of some species may lack a marked pear-shaped outline, yet they are linked with others, more typically pear-shaped, forming a continuum, thus arguably falling within the morphologic range of a single species.

The Mediterranean species

Pyrunculus is distributed world wide, however the number of species is hard to evaluate, even roughly, as it is likely that some species are usually quoted in molluscan check-lists under other genera or families – e.g. *Cylichna* Lovén, 1846, *Retusa*, etc. – and, moreover, it is likely that there are species still awaiting a description, especially in the Indo-Pacific waters (cf. CEDHAGEN, 1997). PILSBRY (1895: 229-233) listed 10 *Pyrunculus* species, yet it may be reasonably argued that the actual representatives of *Pyrunculus* are more numerous. The number of Mediterranean species usually ascribed to the genus is low. The last printed catalogue of Mediterranean molluscs, namely SABELLI et alii (1990-1992: 53, 230, 424), lists 2 species, namely «*Pyrunculus ovatus* (Jeffreys, 1871)» and «*Pyrunculus minutissimus* (Monterosato, 1878)». In the past other *Pyrunculus* species were quoted for the Mediterranean. LOCARD (1897: 71; 1905: 56) recorded *Cylichna obesiuscula*, erroneously ascribed to Monterosato, who never quoted this species in his works, the actual authorship of this name being by BRUGNONE (1877). *Cylichna obesiuscula* had been introduced for Sicilian fossil material, being already ascribed to *Pyrunculus* by PILSBRY (1895: 231-232) together with *Cylichna ovata* Jeffreys (which we regard as conspecific, see below). Recently, one of the writers (TRINGALI, 1993: 26) noticed that *Bulla hoernesii* Weinkauff, 1868, usually included in *Cylichna*, is a *Pyrunculus*.

We consider that three species are known for the Mediterranean Sea: *Pyrunculus ovatus* (Jeffreys in W.B. Carpenter & Jeffreys, 1871), *P. hoernesii* (Weinkauff, 1866), and *P. fourierii* (Audouin, 1827), the former possibly being extinct in the Mediterranean, where only empty shells have been found within deep-water sediments. *Pyrunculus fourierii* is an Indo-Pacific species, inhabiting the Eastern Mediterranean as a Lessepsian migrant. These species and their synonymies are briefly commented in the following notes. *Utriculus minutissimus* MONTEROSATO, 1878 (: 159-160), included in this genus by NORDSIECK (1972: 36; 237, fig.15), and later checklists (PIANI, 1980: 159; BRUSCHI et alii, 1985: 33; SABELLI et alii, 1990-92: 53, 230, 424; BEDULLI et alii, 1995: 6), must be removed from *Pyrunculus*. It is actually a *Retusa*, according to the evenly cylindrical shell with flat or protruding spire (Figs. 34a-b), and the gizzard plates typical of the genus (for a more detailed discussion on *Retusa minutissima* see OLIVERIO & TRINGALI, 2001, this Volume). It is likely that the above mentioned authors were misled by NORDSIECK (1972), who figured under *Utriculus minutissimus* an apparent *Pyrunculus*, which, however, does not fit the original description and type material.



Figs. 15-27. Retusid shells - **Fig. 15:** *"Pyrunculus"* sp., (Tertiary ?) Fossil deposits of Altavilla Milicia (Palermo, Sicily), (identified by Monterosato as *«Coleophysis* [illegible] n. sp.») (Monterosato coll.). **Figs. 16-21:** *P. hoernesii* (Weinkauff) – **Fig. 16:** syntype, Algiers (Algeria), unrecorded depth (Monterosato coll.) (h.: 2.8 mm); **Figs 17-20:** material labelled as *«Cylichna cuneata»* by Tiberi (**Figs. 17-19:** Gulf of Naples, unrecorded depth. (Fig. 17 h: 5.6 mm); **Fig. 20:** Taranto, (Southeast Italy, Pleistocene deposits) (h.: 3.7 mm) (Monterosato coll.); **Fig. 21a-21b:** West Sahara, between 24°-25° N. lat., 40-50 m, from stomach of sole fishes (F. Gubbioli leg.). **Fig. 22:** *"Retusa"* sp., labelled as *«Cylichna conuloides* S. Wood» by R.B. Watson, Suffolk (U.K.), coralline crag Fossil deposits (Monterosato coll.) (h.: 3.2 mm). **Figs. 23-26:** *P. fourierii* (Audouin) – **Figs. 23a-b, 24, 25:** Soguksu (Aydincik, South Turkey), 9-10 m *Posidonia oceanica* intermatte's sediment (RV leg.) (Figs. 24-25 respective h: 3.0; 3.2 mm); **Fig. 26:** Northern coast of Green Is. (Cairns, Queensland), coral reef sediment 3-4 m (C. Schander leg.). **Fig. 27:** *Retusa dilatata* Pallary, syntype, Sfax, (Tunisia) (P. Pallary leg., Monterosato coll.) - **Scale bars:** 1.0 mm (15, 18, 19, 21b, 23a-b, 26, 27); 500 µm (21a).

Pyrunculus ovatus **(Jeffreys in W.B. Carpenter & Jeffreys, 1871)**
(Figs. 1-14, 33, 35a-b, 45)

- *Bulla conulus* Deshayes, 1824, sensu Auctores
- *Cylichna umbilicata* var. "*conulus*" Jeffreys, 1867 (: 414-415)
- *Cylichna ovata* Jeffreys in W.B. Carpenter & Jeffreys, 1871 (: 156)
- *Cylichna obesiuscula* Brugnone, 1877 (: 39-40; pl. 1, fig. 7)
- (?) *Cylichna obscura* Sykes, 1904 (: 37; pl. III, figs. 9-9a)

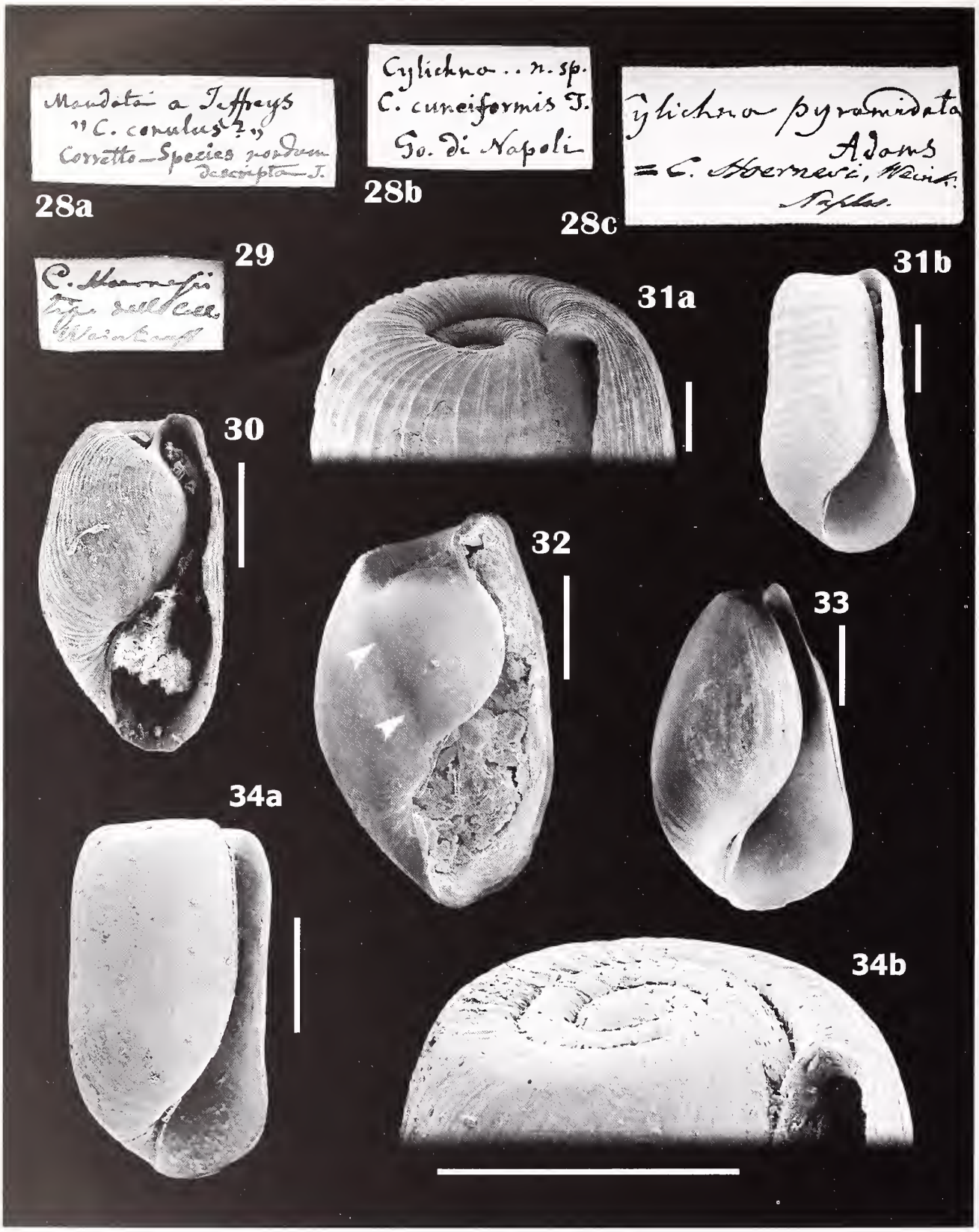
Material examined - Type material: *Cylichna ovata*, not examined; «holotype» figured by Warén (1980: pl. 6, fig. 14) (USNM). *Cylichna obesiuscula*, Ficarazzi (Palermo, Sicily, probably Pleistocene), 1 sh. (syntype), (Monterosato coll., box 16142, ZMR); Ficarazzi (Palermo, Sicily, probably Pleistocene), 207 shs. + 2 frgs. (syntypes), (Monterosato coll., box 16121, ZMR); Mt. Pellegrino (Palermo, Sicily, probably Pleistocene), 2 shs. (syntypes) (Monterosato coll., box 16142, ZMR). *Cylichna obscura*: not examined (probably in the NHML). **Other material:** Mediterranean Sea: Oran (Algeria), unrecorded depth, 1 sh. (P. Pallary leg., Monterosato coll., box 16335, ZMR); "De Profundis" Cruise (1991), Stn. DP91-4, Eastern Sardinia, 571-347 m, over a hundred shs. (cf. Bonfitto et alii, 1994: 148; 156, fig. 25); Terracina (Latina, West Italy), 600 m, muddy residuals inside a Roman amphora, 1 sh. (Roberto Ardovini coll., Rome). Northeast Atlantic: "Triton" exp. (1881) between the Hebrides and Faeroes Islands, Stn. 13, 555 fathoms, 2 shs., (Monterosato coll., box 16102, ZMR); "Princesse Alice" exp. (1895), Stn. 46, 1385 m, 50 shs. (labelled by Dautzenberg, Monterosato coll., box 16102, ZMR); "Talisman" exp. (1883), Stn. 127, Azores, between Pico and St. Georges., 1258 m, 18 shs. + 1 frg. (probably sent by A. Locard, Monterosato coll., box 16102, ZMR); Mauritania, from fishing net residual, 900-1200 m, 1 partly preserved spm. (Franco Gubbioli coll., Marbella). Italian fossil deposits: Rometta (Southwest Italy, probably Pleistocene), 2 shs. identified by Brugnone as «*Cylichna obesiuscula*» (Monterosato coll., box 16142, ZMR); Castellace, (Southwest Italy, probably Pleistocene), Lower Pleistocene deposit near the Boscaino Torrent, , 1 sh. (LPT coll., Rome)

Remarks - This species has been frequently misidentified, especially in the nineteenth century, as *Bulla conulus* Deshayes, 1824 (: 41; pl. V, figs. 34, and 36), an Eocene-Miocene *Pyrunculus* species of the Paris basin, although the latter has spiral lines on the basis, lacking on *P. ovatus*, and a more slender outline. The first author who recognised this entity as distinct was Jeffreys (1867), who described it as a simple var. "*conulus*" of *Retusa umbilicata* (Montagu, 1803), underlying, however, that he considered this variety as distinct from *Bulla conulus* Deshayes. Later on, however, Jeffreys in W.B. Carpenter & Jeffreys (1871) introduced the name *Cylichna ovata* by means of a vague reference to «*Bulla conulus*, S. Wood, not Deshayes (Coralline Crag)». It is actually difficult to identify the fossil shells from Sutton (Britain) described and figured by Wood (1848: 173-174; pl. XXI, figs. 2a-c) under the name *Bulla conulus* Deshayes, with the present species. Possibly Wood's shells – not examined by us - are not the same of *P. conulus*, but they show a fine spiral sculpture all over the shell which should not apply to *P. ovatus*, and a more rounded top. We have examined three shells from the Coralline Crag deposits of Suffolk (Britain) labelled as «*Cylichna conuloides* S. Wood» by R.B. Watson (Monterosato coll., box 16122, ZMR), which could match better Woods' material, looking closer some *Retusa* species with sunken spire (Fig. 22). According to the ICZN (1999: Art. 72.4)) the material on which the drawing and description by Wood are based attained the status of type material of the new species along with the original material in Jeffreys' hands when the new species was recognised. Nevertheless Warén (1980: 36; pl. 6, fig. 14) considered as the «holotype» of *P. ovatus* the single shell from Deal Voe (Shetland Islands) in the Jeffreys coll.(USNM, no. 175405) thus making a valid selection of a lectotype (ICZN, 1999: Art. 74.6). Since the shells of Wood may prove not conspecific with the Quaternary *P. ovatus*, this designation would stabilise usage of *P. ovatus*.

Pyrunculus ovatus is an amphiatlantic gastropod, moderately common on muddy bottoms in deep waters. This species has been recorded by several authors for the Northeast Atlantic (e.g. Dautzenberg, 1889: 23; Jeffreys, 1883: 393; Locard, 1897: 69-71) being also known for the Northwest side (e.g. Dall, 1889: 86; Verrill, 1881: 382, as «*Diaphana conulus* (Deshayes)»; Watson, 1886: 664; pl. XLIX, fig. 9). It is a member of the Atlantic fauna, whereas it has never been recorded alive in the Mediterranean, where records are probably based on late Pleistocene fossils only. The first Mediterranean record was by Jeffreys (1882: 34), based on material collected by the Italian Vessel "Washington" (1881 exp.) in the Central Mediterranean basin. Also the old Mediterranean record of *Cylichna obesiuscula* Brugnone by Locard (1897: 71; 1905: 56) after a single shell from off Marseille (South France) is to ascribe to *P. ovatus* (*Cylichna obesiuscula* is a swollen form of *P. ovatus*). More recently, Bonfitto et alii (1994: 148; 156, fig. 25) figured and identified as «*Pyrunculus* sp.» a lot of swollen shells of *P. ovatus* collected by the R/V "Bannock" ["De Profundis" 1991 expedition, Stn. DP91-4, East Sardinia, 571-347 m].

The shell is by far the most variable in shape of all the Mediterranean *Pyrunculus*. In the typical form, as represented by the lectotype, the outline is evenly conical, with nearly flat sides, and a broad base. The maximum diameter is at about the lower third of the height; yet there are shells with the maximum diameter closest to the base, and others more swollen in the middle, thus with evenly rounded sides. Those more oval shells may, moreover, display a variable outline, from slender to somewhat stumpy. Also the spire may vary: it is usually deeply sunken, with a narrow apical umbilicus; however, the latter, may be occasionally larger, clearly displaying the spire in upper view. The apical umbilicus is always encircled by a marked ridge. The columella may bear a weak fold, which is usually lacking. The shell surface is nearly smooth, moderately shining on fresh shells, and occasionally also on fossil ones. It is sculptured by weak growth lines only, lacking any spiral sculpture.

Cylichna obesiuscula Brugnone seems to fall within the morphological range of *P. ovatus*, representing the more rounded, egg-shaped and swollen form, linked to the typical, pear-shaped form by all intermediates. Traditionally, *Cylichna obesiuscula* has been regarded as a full valid species (Jeffreys fide Brugnone, 1877; Monterosato in schedis, cf. Locard, 1897: 71; Seguenza, 1880: 252; Dall, 1889: 86; Pilsbry, 1895: 231-232; Locard, 1897: 69-71, 1905: 56; Bouchet, 1975: 334). However, examining a large number of shells, a different view arises. The rich lot of syntypes from Ficarazzi shows a predominance of swollen shells with rounded sides, yet it contains a wide range of forms, including intermediates to typical *P. ovatus*. Therefore *Cylichna obesiuscula* seems to be a form of *P. ovatus*. The couple of shells from the "Triton" exp. (1881), Stn. 13, are not labelled by Jeffreys, although arguably they were sent by the British malacologist himself to Monterosato as representatives of



Figs. 28a-c: original labels of *Cylichna cuneata* Tiberi. **Fig**. 29: label by Monterosato for the syntype of *P. hoernesii* (Weinkauff). **Fig**. 30: *P. fourierii* (Audouin), juvenile shell, Soguksu (Aydincik, Turkey), *Posidonia oceanica* intermatte's sediment 10 m (RV leg.). **Figs**. 31a-b: *Retusa desgenettii* (Audouin), Marsa Fijab (Sudan), beached (MO leg.). **Fig**. 32: *P. hoernesii* (Weinkauff), juvenile shell, West Sahara, between 24°-25° N. lat., 40-60 m (F. Gubbioli leg.) (arrows point to the protoconch-teleoconch boundary). **Fig**. 33: *Pyrunculus* ovatus, syntype of *Cylichna obesiuscula* Brugnone, Ficarazzi (Palermo, Sicily) (Monterosato coll.).**Figs**. 34a-b: *Retusa minutissima* (Monterosato), Paleohora, Crete, bioclastic sand sample 10 m (S. Farinelli leg.) - **Scale bars:** 1.0 mm (33); 500 µm (31b, 34a-b); 200 µm (30, 31a, 32).

P. ovatus (JEFFREYS, 1883: 393, lists this species from Stn. 13). Anyway, they cannot be regarded as type material, having been collected after the original introduction of the species. These shells belong to a slender oval form, observed also within the material from the "Princesse Alice" exp. (1895), as well as within the type material of *Cylichna obesiuscula*. As *C. obesiuscula*, this form is not truly pear-shaped, being somewhat oval, and would be characterised by a more slender outline and a slightly broader apical umbilicus. We find, however, that also this form belongs to the morphological range of *P. ovatus* as an extreme. Arguably it is the same of the Northeast Atlantic *Cylichna obscura* Sykes, 1904, described from the "Porcupine" exp. (1869-1870) Stn. 3. Since we have not examined the relevant type material, we prefer to keep a provisional question mark on the synonymy with *P. ovatus*.

The gizzard plates of *P. ovatus* were described and sketched by BOUCHET (1975: 333, figs. 6b-c). We have examined two paired plates only from partially preserved dry residuals of a West African specimen (Figs. 35a-b); the unpaired plate was already lost by the damaged specimen. Both are typical *Pyrunculus* paired plates. BOUCHET (1975: 332) noticed that *P. ovatus* feeds on Foraminifera as most of the carnivorous cephalaspideans (cf. CEDHAGEN, 1996). Thus it was not surprising to find several foraminiferan tests (exemplified in the Figs. 40-44), inside the dry residuals of the gizzard of our specimen.

Pyrunculus hoernesii **(Weinkauff, 1866)**
(Figs. 16-21, 32, 37a-b, 46, 50a-c)

- *Bulla striatula* Forbes, 1844 sensu Auctores
- *Bulla conulus* Deshayes, 1824, sensu WEINKAUFF (1862: 337)
- *Bulla (Cylichna) hoernesii* WEINKAUFF, 1866 (: 238)
- *Cylichna cuneata* TIBERI, 1868 (: 180)

Material examined - Type material: *Bulla hoernesii*: Alger (Algeria), unrecorded depth, 1 sh. (syntype) (ex Weinkauff coll., Monterosato coll., box 16118); further material probably in the USNM, not examined. *Cylichna cuneata*: not identifiable (see below). **Other material:** Mediterranean Sea: Terracina (Latina, West Italy), muddy residue from fishing net, 300 m depth, 1 sh. (Roberto Ardovini coll., Rome); Gulf of Naples, 223 shs./spms./frgs. labelled as «*Cylichna* n. sp., *Cylichna cuneiformis* T., Go. di Napoli» by Tiberi (Monterosato coll., box 16118; see Figs. 28a-c); Capri Is. (Naples, Southwest Italy), 1 sh. (Monterosato coll., box 16118); Palermo (West Sicily), 22 shs. (Monterosato coll., box 16028); Cape San Vito (West Sicily), 25 shs./spms. (Monterosato coll., box 16118); Vendicari Is. (West Sicily), bioclastic sand sample 30 m, 1 sh. (LPT coll., Rome); Algiers (Algeria), 28 shs./spms. (P. Joly leg., Monterosato coll., box 16118); Oran (Algeria), 2 shs. (P. Pallary leg., Monterosato coll., box 16335); Cala Iris (Torres de Alcalá, North Morocco), bioclastic sand sample 2-10 m, 8 shs./frgs. (LPT coll., Rome). Libyan coasts 1 sh.; It-Trozz (Malta Is.), bioclastic sand sample 130 m, 1 sh. (RV coll., Rome). Northeast Atlantic: Pta. De Teno, (Tenerife Is., Canary Islands), bioclastic sand sample 27 m, 2 shs. (LPT coll., Rome); Punta Blanca (Puerto Santiago, Tenerife Is., Canary Islands), bioclastic sand sample 30 m, 9 shs. (LPT coll., Rome); West Sahara, 24°-25° N, stomach contents of flatfishes (Fam. Pleuronectidae) 16 spms./shs. (Italo Nofroni, Mauro Pizzini and LPT colls., Rome). Italian fossil deposits: Taranto (Southeast Italy, probably Pleistocene), 1 sh. labelled as «*Cylichna cuneata*» by Tiberi (Monterosato coll., box 16118); Gravina, (Southeast Italy, probably Pleistocene), 1 sh. labelled as «*Cylichna cuneata*» by Tiberi (Monterosato coll., box 16118);

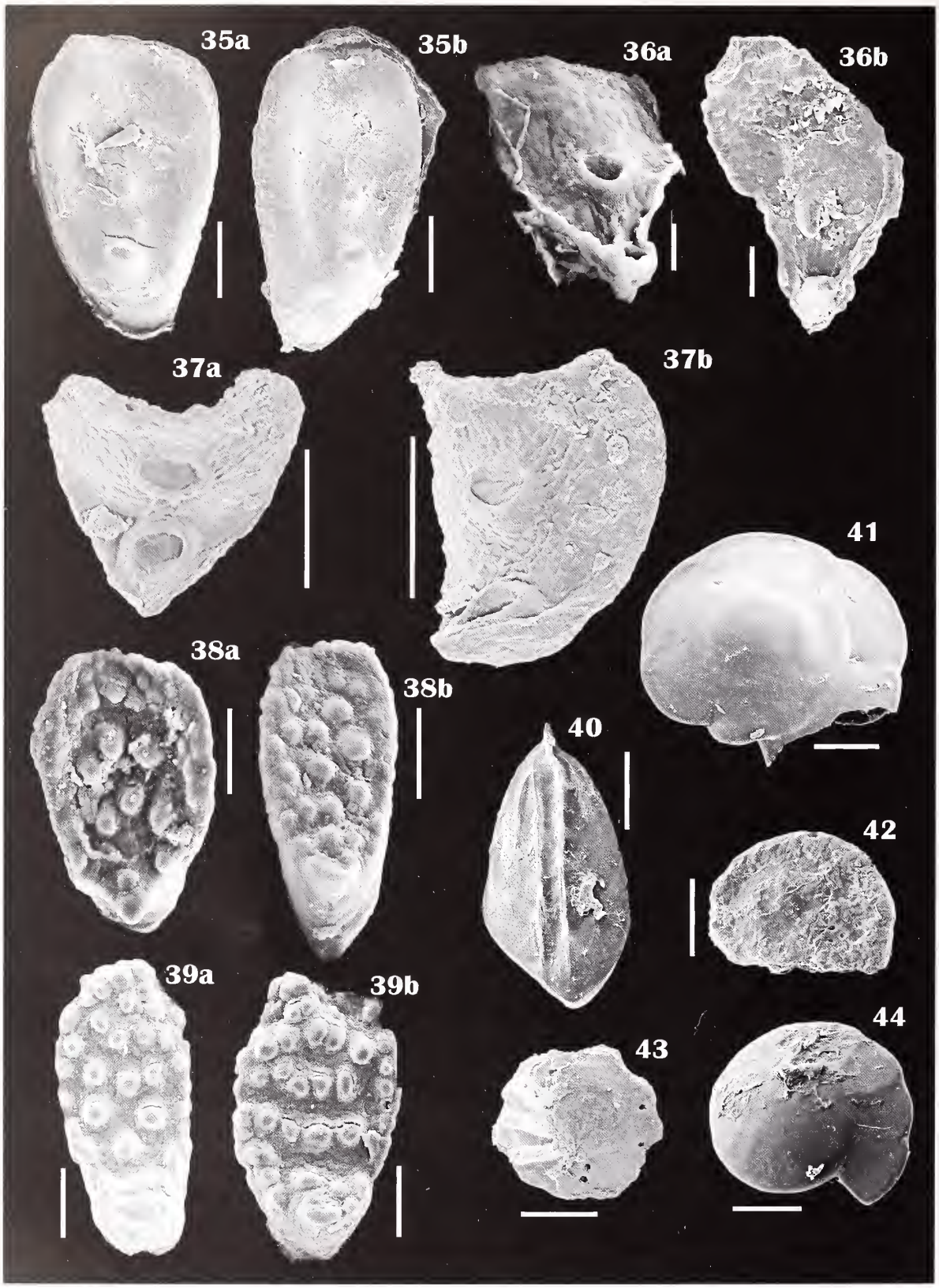
Remarks - The identity, nomenclature, systematic position, and geographic range of this species has been already discussed elsewhere (TRINGALI, 1993; 1995).

The shell of *Pyrunculus hoernesii* is more slender and evenly conical than *P. ovatus*, with quite flat sides, less variable in outline, and of more moderate size (height up to 5-6 mm, but usually smaller). It is quite characteristic in its weak axial ribs, evident on the top "crown", and gradually vanishing downward. Such an axial sculpture recalls that of *Retusa truncatula* (Bruguière; 1792), yet the nearly shining surface of fresh shells is also run by simple spiral lines, which are nearly lacking on the middle, and more closely spaced toward the base. Two more marked spiral lines run just below the top. Conical shells of *R. truncatula* show a weak, rounded recess just above the middle, that gives a more sinuous outline to the shell, never seen in *P. hoernesii*.

The morphology of gizzard plates (Figs. 37a-b) proves *P. hoernesii* to be a *Pyrunculus* (cf. TRINGALI, 1993: 26; 28, figs. 3-7; MORENO & TEMPLADO, 1998: 51, figs. 22-23). Observed through the SEM some unpaired plates displayed evident cavities inside the tubercles. Being dry preparations for the SEM, we can not rule it out that these cavities could be artefacts due to dehydration. As *P. ovatus*, it feeds on foraminiferans (Fig. 49).

Pyrunculus hoernesii inhabits sandy-muddy bottoms from shallow waters down to the upper slope (300-400 m ca.), in the whole Mediterranean basin, possibly being more frequent along the Southern coasts. It lives also in the neighbouring Atlantic waters (Northwest Africa: DAUTZENBERG, 1917: 65; PALLARY, 1920: 20; TRINGALI, 1993: 24; West Spain: SYKES, 1904: 36; Canary Islands: TRINGALI, 1995). It is a rather common species within its range.

WEINKAUFF (1866: 238) introduced the name *Bulla hoernesii* in an addition to his check-list of the Algerian marine molluscs, by a reference to two drawings published by HÖRNES (1856: 620; pl. 50, figs. 4a-b) as «*Bulla conulus* Deshayes, 1824». We have not examined the fossil shell sketched by HÖRNES (1856). They have the status of type material by means of WEINKAUFF's (1866) reference, according to the ICZN (1999: Art. 72.4). It is difficult to say whether the Recent material from Algiers which Weinkauff had in his hands really matches that Tertiary material from the Vienna Basin. The figured shell is similar to *P. hoernesii*, yet it shows more marked and close set axial and spiral sculpture, and it seems closer to the fossil shell from Altavilla Milicia (Palermo, Sicily) here figured (Fig. 15). Anyway, as in the case of *Cylichna ovata*, we consider that the Algerian shells in Weinkauff's hands were decisive to establish the introduction of a new species, and therefore belong to the type material of *P. hoernesii*. After the common usage of Weinkauff's name in recent literature for the species herein discussed, the selection of a lectotype among Weinkauff's material would be desirable to stabilise the identity of the name. We avoid the designation as lectotype of the single syntype in the ZMR, preferring a selection from the material, probably richer, in the USNM, where the Weinkauff coll. arrived as a part of the Jeffreys coll.



Figs. 35-44. Retusid gizzard plates and preyed foraminiferans - **Figs. 35a-b**: *P. ovatus* (Jeffreys), paired pls., Mauritania, 900-1200 m (from the shell in Fig. 11), **Figs. 36a-b**: *P. fourierii* (Audouin), Monoa Bay (Palawan Is., Philippines), coral reef sediment 11 m (a: unpaired g. pl.; b: paired g. pl.; from a shell with a h: 1.5 mm ca.) ; **Figs. 37a-b**: *P. hoernesii* (Weinkauff), unpaired pl., two different views, West Sahara (data as Figs. 21a-b, from a shell with a h: 2 mm ca.), **Figs. 38a-b**: *R. mamillata* (Philippi), Stn. AKD.92-22 (a: unpaired g. pl.; b: paired g. pl.; from a shell with a h: 2.5 mm ca.); **Figs. 39a-b**: *R. desgenettii* (Audouin), Marsa Fijab (Sudan), beached (a: paired g. pl.; b: unpaired g. pl.; from a shell with a h: 2 mm ca.); **Figs. 40-44**: foraminiferan tests from the gizzard contents of *P. ovatus* (Jeffreys), Mauritania, 900-1200 m (from the shell in Fig. 11) - **Scale bars**: 100 µm (35a-b, 37a-b, 40, 41, 42, 43, 44); 20 µm (36a-b); 50 µm (38a-b; 39a-b).

Despite that this species has been frequently identified as *Bulla striatula* Forbes, 1844 (e.g. Monterosato, 1884: 142), this name cannot be employed, because the original description (Forbes, 1844: 188), and the drawing of a «type» (a syntype, or the holotype?) found in the British Museum published by Sykes (1904: pl. III, fig. 3) do not apply to the species herein discussed. It is likely that *Bulla striatula* is a junior synonym of *Retusa mamillata* (Philippi, 1836) (Jeffreys, 1867: 421; see also Tringali, 1993: 24), although Sykes (1904: 37) noticed that the type has a rather sunken protoconch, not showed on the drawing. *Retusa mamillata* (Philippi, 1836) is a valid Northeast Atlantic-Mediterranean species, not a simple form of *Retusa truncatula* (Bruguière, 1792) as erroneously suggested by Lemche (1948: 55). It has a very variable spire, ranging from a *Tornatina*-like prominence to a somewhat deep immersion (Figs. 51-52). In fact Sykes (1904) did not contend that the type of *Bulla striatula* could be *R. mamillata*, and anyway noticed that it was not the same of *P. hoernesii*, as it is evident. More recently Grossu (1986: 429-430, figs. 198a-b) and other East European authors adopted the name «*Retusa (Coleophysis) striatula* (Forbes)» for a form related to *R. truncatula*, a view on which we disagree.

Cylichna cuneata Tiberi, 1868, applies also to *P. hoernesii*, as Tiberi himself noticed when placing a new label on the box where his material of *C. cuneata* is kept (he considered, in turn, *P. hoernesii* a synonym of the Chinese *Bulla pyramidata* A. Adams, 1850). *C. cuneata* was introduced with a clear description based on a single shell or specimen from the Gulf of Naples. The holotype was not marked by Tiberi. The material of Tiberi, now in the Monterosato coll., includes many mixed shells/specimens from the Gulf of Naples, all conspecific, labelled by Tiberi as «*Cylichna cuneiformis*» (obviously the manuscript name originally employed by Tiberi before the original description) kept all together in a tube. Thus, it can not be decided which is the holotype, but the identity of *C. cuneata* is evident. More problematic is the relationship with the Western Atlantic *Cylichna caelata* K.J. Bush, 1885, described from Cape Hatteras (North Carolina, East U.S.A.), and ascribed to *Pyrunculus* by Pilsbry (1895). De Jong & Coomans (1988: 209, fig. 693) published under the name «*Cylichna caelata* Busch», the SEM photo of a shell from Suriname which has a shape closely similar to *P. hoernesii*. However, the spiral lines of *Pyrunculus caelatus*, described by Bush (1885) as «punctate» ("pitted"), do not fit the simple spiral lines of *P. hoernesii*.

Pyrunculus fourierii (Audouin, 1827)
(Figs. 23-26, 30, 36a-b, 47)

- *Bulla fourierii* Audouin 1827 (: 178)
- (?) *Bulla decussata* A. Adams, 1850 (: 595; pl. CXXV, fig. 147)
- (?) *Utriculus simillimus* R.B. Watson, 1883 (: 340)
- (?) *Cylichna protumida* Hedley, 1903 (: 396-397; fig. 112)
- *Retusa dilatata* Pallary, 1904, sensu Bogi & Khairallah (1987: 56)
- *Retusa dilatata* var. *minor* Pallary, 1904, sensu Bogi & Khairallah (1987: 56)

Material examined - Type material: *B. fourierii*, not examined; the holotype (MNHN) is figured by a SEM photo in Bouchet & Danrigal (1982: 20, fig.54). *Bulla decussata*: not examined (probably NHML). *Utriculus simillimus*: not examined (probably NHML). *Cylichna protumida*: not examined (probably AMS). **Other material:** Eastern Mediterranean: Soguksu (Aydincik, Southern Turkey), *Posidonia* intermatte's sediment 9 m, 15 shs. (Raimondo Villa and LPT colls., Rome), and 10 m, 3 shs. (LPT coll., Rome); Kash (Southern Turkey, AKD'92 exp., see Oliverio et alii., 1993), Stn. AKD-22, bioclastic sand sample 34 m, 6 shs. Indo-Pacific: "La Grand Baie" beach (Mauritius Is.), coral reef sediment 2 m, 1 sh. (LPT coll., Rome); Pee-Pee Is. (Andaman Islands), coral reef sediment 30 m, 1 sh. (LPT coll., Rome); Honda Bay (Palawan Is., Philippines), coral reef sediment 11 m, 3 partially preserved spm. + 30 shs. (IN coll., Rome); Northern coast of Green Is. (Queensland, Australia), coral reef sediment 3-4 m, 2 sh. (LPT coll., Rome).

Remarks - The name *Bulla fourierii* was introduced by reference to a drawing on the plates on Egyptian molluscs by J.-C. Savigny (see also Pallary, 1926: pl. IX, fig. 6), and has been employed, with very few exceptions, in the Red Sea literature, and, more recently, in some Mediterranean works. However, this species is widespread through the Indo-West Pacific Region. We examined a scarce Indo-Pacific material of *P. fourierii*, yet from quite far localities. Some names are probably junior synonyms of *P. fourierii*. The Australian *Utriculus simillimus* Watson, 1883, and *Cylichna protumida* Hedley, 1903, seem to belong to this species after the original description and drawings; for *U. simillimus*, probably based on subadult shells, see also the drawing in Watson (1886: pl. XLIX, figs. 2b-c). The original description and drawing of the Chinese *Bulla decussata* A. Adams, 1850, is less clear. However Kuroda & Habe (1954: pl. 2, fig. 5) published a photo of a shell of *B. decussata* recovered in the P. Carpenter coll. (Redpath Museum of McGill Univ., Montreal) much probably donated by A. Adams himself, which obviously fits *P. fourierii* shell morphology. Although this is not a syntype, originating from Japan, *Bulla decussata* is arguably a synonym of *P. fourierii*. As we have not examined their types, the listed synonyms need to be confirmed. Further names (also reported by Kuroda & Habe, 1954: 7) should be checked as possible synyonyms of this species.

Sharing Gaglini's (1991: 5) view, we find untenable the synonymy of *P. fourierii* with both *Retusa dilatata* Pallary, 1904, and *Retusa dilatata* var. *minor* Pallary, 1904, proposed by Bogi & Khairallah (1987: 56). Pallary (1904: 215-216; pl. VII, fig. 8) described *R. dilatata* and its variery *minor* from Sfax (Tunisia), thus from a part of the Mediterranean where there were hardly any Lessepsian migrants by 1900. The examination of some syntype of both forms (Fig. 27, 48a-b) conserved in the Monterosato (box 16049, ZMR), and in the F. Settepassi colls. (no catalogue number, ZMR), shows that *R. dilatata* and its variety *minor* are closely related to *Retusa truncatula* (Bruguière, 1792), possibly a large sized form, with a height up to 7 mm.

Recorded for the Suez Canal (Moazzo, 1939: 133-134), this species has entered the Eastern Mediterranean basin as a Lessepsian migrant - on the concept of «Lessepsian migration» see Por (1978: in particular 87 and following pp.), and Oliverio (1995: 36) – spreading through the Levant Sea. After the first Mediterranean record by Bogi & Khairallah (1987: 56; 60, fig. 5) from the Bay of Jounieh (Lebanon), *P. fourierii* was also recorded along the Mediterranean coasts of Israel, Cyprus Is., and Southern Turkey (e.g. Aartsen et alii, 1989: 71; Buzzurro & Greppi, 1996: 8; Cecalupo & Quadri, 1996: 110; Engl, 1992: 8; 1995: 46;

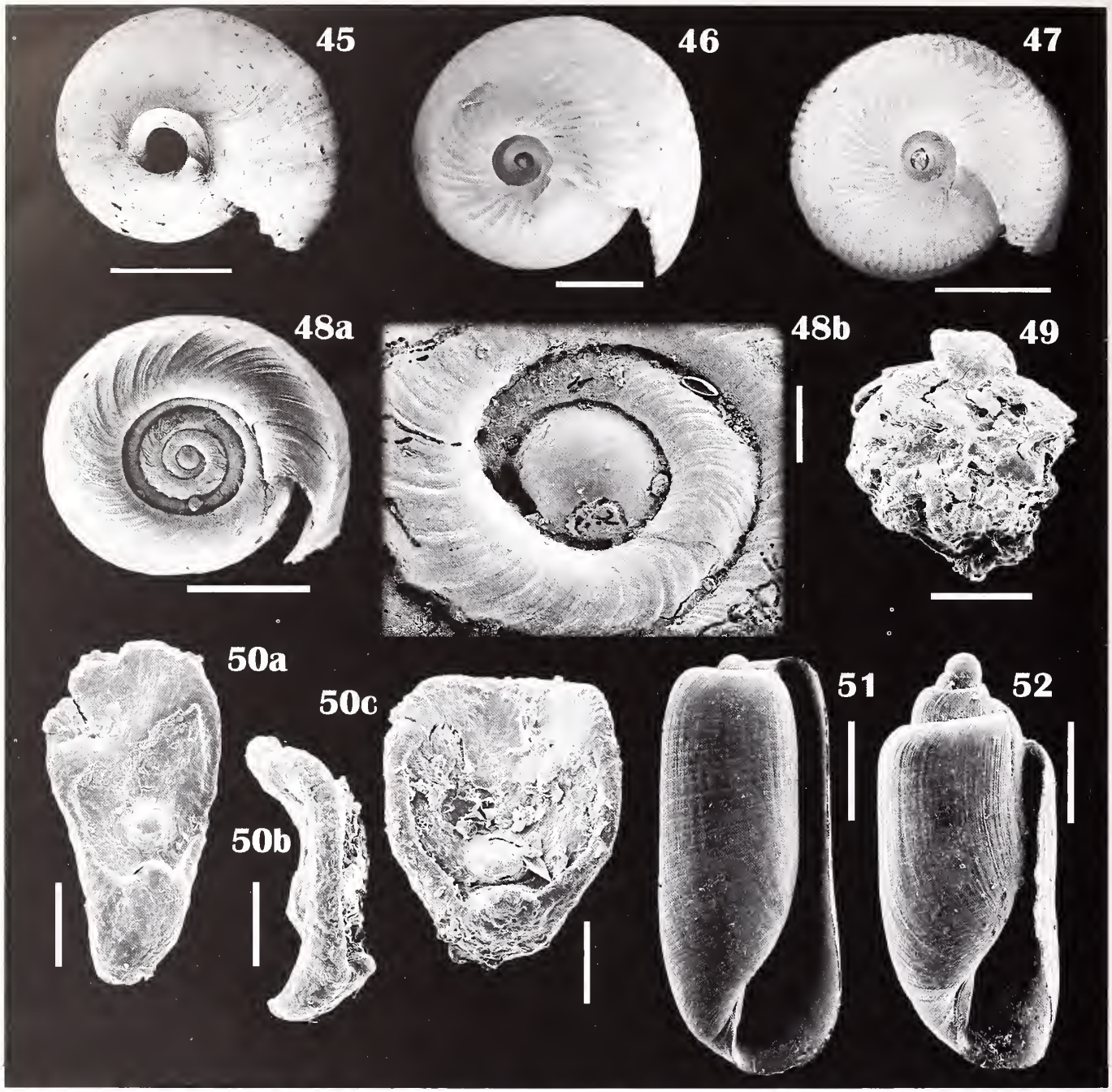


Fig. 45: *P. ovatus* (Jeffreys), syntype of *Cylichna obesiuscula* Brugnone, same shell in Figs. 3a-b, upper view. **Fig. 46**: *P. hoernesii* (Weinkauff), labelled as «*Cylichna cuneata*» by Tiberi, Gulf of Naples (Monterosato coll.), upper view. **Fig. 47**: *P. fourierii* (Audouin), same shell in Figs. 23a-b, upper view. **Figs. 48a-b**: *Retusa dilatata* Pallary, syntype, same shell in Fig. 27, upper view and protoconch. **Fig. 49**: foraminiferan test from the gizzard contents of *P. hoernesii* (Weinkauff), in a specimen labelled as «*Cylichna cuneata*» by Tiberi, Gulf of Naples (Monterosato coll.). **Figs. 50a-c**: *P. hoernesii* (Weinkauff), gizzard plates from a specimen labelled as «*Cylichna cuneata*» by Tiberi, Gulf of Naples (Monterosato coll.) (a: paired g. pl.; b: paired g. pl., lateral view; c: unpaired g. pl.). **Figs. 51-52**: *Retusa mamillata* (Philippi), Stn. AKD.92-No. 22, Kash (Turkey), bioclastic sand sample 34 m. – **Scale bars**: 1.0 mm (45, 48a); 500 µm (46, 47, 51, 52); 200 µm (49); 100 µm (48b, 50a-c).

Tringali & Villa, 1990: 35, 37). It has never been recorded alive in the Mediterranean, yet we have observed scanty residues of soft parts – few brownish spots visible through the shell – inside some shells from Kash and Soguksu (Southern Turkey).

The authors who quoted *P. fourierii* mostly ascribed it to the genus *Retusa*: that is the case of all Mediterranean records, as well as of Dautzenberg (1929: 126 or 332), Moazzo (1939: 133), Pallary (1926: 75), Sabelli et alii (1990-1992), and Vine (1986: 175). The exception is Pilsbry (1895: 311-312), who adopted *Cylichna* Lovén, 1846. Actually, the shell morphology does not allow to give the species a position within *Pyrunculus*, being more similar to *Retusa*: for instance the slightly pear-shaped outline of *P. fourierii*, with its deeply sunken spire, is not dissimilar from that of the Red Sea *Retusa desgenettii* (Audouin, 1827) (Figs. 31a-b), which also shares with *P. fourierii* the same sculpture of close set of spiral and growth lines, crossing each other resulting in a well marked network, shining on

fresh shells under the light. However, a comparison of the gizzard plates proves that *P. fourierii* belongs to *Pyrunculus*, whereas *R. desgenettii* is a true *Retusa* (cf. Figs. 36a-b, 39a-b). We examined dry residues of a damaged specimen of *P. fourierii* from Philippines still keeping two plates only: the SEM photos are unfortunately not good, nevertheless the couple of large tubercles on the plates is evident. Each tubercle of the dry unpaired plate shows a cavity as those noticed for *P. hoernesii*.

CONCLUSIONS

Very few species of *Pyrunculus* are known in the Northeast Atlantic-Mediterranean waters. The genus was omitted by SETTEPASSI et alii (1976), whereas of the two species quoted by PIANI (1980), BRUSCHI et alii (1985), SABELLI et alii (1990-1992), BEDULLI et alii (1995), only *P. ovatus* has been retained here as a Mediterranean *Pyrunculus*. *Utriculus minutissimus* has been moved to *Retusa*. On the other hand, *P. hoernesii* and *P. fourierii* have been removed respectively from *Cylichna* and *Retusa* to be added to the list of Mediterranean *Pyrunculus*.

The occurrence of *P. ovatus* as living in the Mediterranean Sea is still to prove: all records may be based on fossils. Also *P. fourierii* has not been recorded on living specimens so far (SABELLI et alii, 1990-1992: 423), although the large number of shells suggests its acclimatisation in the Levant Sea.

The selection of a lectotype for *Bulla hoernesii* among Weinkauff's material in a next future is strongly recommended in order to definitely set the use of this name. Finally, some names have to be checked as synonyms of *P. fourierii* and *P. hoernesii* after examination of the relevant type material.

Much investigation is still needed to gain a more comprehensive knowledge on the systematics of the Northeast Atlantic-Mediterranean retusid gastropods. Retusidae seems to be one of the cephalaspidean groups where shell morphology is least helpful to define both specific and supraspecific systematics. This fact emerges also in the present work, considering the problematic reference of species to distinct retusid genera after studying the shell morphology alone, as is shown by the case of *P. fourierii*.

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Aposematic coloration and mimicry in opisthobranch mollusks: new phylogenetic and experimental data

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KEY WORDS: Aposematic coloration, mimicry, phylogenetics, nudibranchs

ABSTRACT Expression of aposematic color patterns in opisthobranchs is more prevalent and more overtly manifested in more derived rather than more basal taxa. This is the case in clades such as *Thuridilla*, *Siphopteron*, *Flabellina* and *Halgerda*. In other instances, one taxon is cryptic and its sister taxon exhibits aposematic coloration. Generally, closely related species have similar color patterns, but in one clade of *Flabellina*, four closely related species have strongly divergent color patterns. Sympatric species with similar color patterns result from both descent from a common ancestor as well as from convergent evolution. Contemporary phylogenetic analytical methods provide a basis for distinguishing evolution of similar color patterns between common descent and homoplasy. Species-specific differences in palatability of similarly colored prey for different predators blur traditional distinctions between Batesian and Müllerian mimicry. Additional studies on other mimicry complexes to determine whether these patterns are more generalized need to be undertaken.

RIASSUNTO L'espressione di pattern cromatici aposematici negli opistobranchi sembra essersi maggiormente affermata in taxa "derivati" piuttosto che "basali". Questo è evidente in cladi quali *Thuridilla*, *Siphopteron*, *Flabellina* and *Halgerda*. D'altra parte, un taxon può presentare una colorazione criptica e la sua "specie sorella" avere una colorazione aposematica. Di norma, specie filogeneticamente affini hanno pattern cromatici simili, ma in un clade di *Flabellina*, quattro specie strettamente imparentate mostrano una colorazione fortemente divergente. Specie simpatriche, pur presentando una colorazione simile, possono derivare sia da un antenato comune che essere la conseguenza di un'evoluzione convergente. Gli attuali metodi d'analisi filogenetica permettono di distinguere se un pattern cromatico derivi da un processo evolutivo diretto o sia dovuto ad un fenomeno di convergenza. Differenze specie-specifiche tra specie a pattern cromatici simili nell'appetibilità da parte di predatori diversi rendono meno chiara la tradizionale distinzione tra mimetismo batesiano e mulleriano. Nuovi studi su altri complessi mimetici saranno comunque necessari per definire se tali processi siano più generali di quanto ritenuto fino ad oggi.

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INTRODUCTION

Opisthobranch mollusks have been shown to be excellent study organisms for illustrating the phenomenon of aposematic coloration (Ros, 1977; Edmunds, 1987, 1991; Gosliner & Behrens, 1990; Rudman, 1991). Although Edmunds questioned whether aposematic coloration as an evolutionary strategy has been adequately demonstrated in opisthobranchs, Gosliner & Behrens (*op. cit.*) suggested that the criteria for demonstration had been met. Studies on the chemical nature of secondary metabolites (Faulkner & Ghiselin, 1983; Cimino & Ghiselin, 1998, 1999; Avila, 1995) strongly support the idea that opisthobranchs have employed sequestered chemical compounds as a primary defensive strategy. Utilization of chemical defense mechanisms by opisthobranchs represents a major divergence from other heterobranchs and other gastropod taxa where the molluscan shell provides the primary defense against predation (Vermeij, 1978). Species-level phylogenetic hypotheses of various opisthobranch taxa recently have provided new data by which evolution of color patterns in various opisthobranch lineages may be examined (Gosliner & Kuzirian, 1990; Gosliner & Willan, 1991; Gosliner & Johnson, 1994, 1999; Gosliner, 1995; Fahey & Gosliner, 1999). Recent studies of opisthobranchs in tropical regions have demonstrated that opisthobranchs and other organisms, especially polyclad flatworms, have similar color patterns and potentially form mimicry complexes (Gosliner & Behrens, 1990). Little evidence has been presented to suggest whether these organisms with similar color patterns are palatable to predators and whether they are differentially palatable to various potential predators. These issues relate directly to the question of whether these apparent mimicry complexes are functional with regard to predator/prey interactions and whether they represent cases of Batesian or Müllerian mimicry.This paper presents evidence of the nature of color pattern differentiation in several distantly related clades of opisthobranchs to determine the array of evolutionary strategies found in opisthobranchs. Similarly, results from field and laboratory feeding experiments using similarly colored opisthobranchs and flatworms as experimental subjects are presented.

MATERIAL AND METHODS

Phylogenetic studies were undertaken employing the methodology described in individual papers that are cited. In general, morphological data sets were analyzed using versions of Paup (Phylogenetic Analysis Using Parsimony) (Swofford, 1993). In some instances (e.g., Gosliner & Johnson, 1999), distinctive color data were included in the construction of the original phylogenetic hypotheses, while in other cases (Gosliner & Willan, 1991) they were not. In each case discussed, the basic assumptions about inclusion or exclusion of characters related to color are explicitly stated. In all cases where color characters were included, tree topology was not markedly altered from the case where these char-

acters were excluded. Rather, greater resolution of polytomies within clades resulted. Field observations of attempted predation were undertaken by direct observation using mask and snorkel in shallow-water habitats and SCUBA for deeper-water situations. Laboratory experiments focused primarily on eliciting feeding responses on opisthobranchs using a variety of predators. Experimental subjects included the nudibranch species *Chromodoris annae* Bergh, 1877, *C. magnifica* (Quoy & Gaimard, 1832), *Phyllodesmium briareum* (Bergh, 1896) and *Flabellina riwo* Gosliner and Willan, 1991 as well as the sacoglossan *Plakobranchus* sp. All specimens of these species were collected in the vicinity of Madang Lagoon, Papua New Guinea during 4-11 August 1989. In other cases, predation experiments were conducted upon a nudibranch/flatworm pair where both individuals share a similar color pattern. These experiments focused primarily upon the nudibranch *Chromodoris preciosa* (Kelaart, 1858) and the polyclad flatworm *Pseudoceros* sp. (Fig. 1A). Specimens of both species were observed in their natural habitat in 1-2 meters of water in Kranket Lagoon, Madang, Papua New Guinea on 12 August 1989. Individuals of both species were abundant and were found within 5-10 cm of each other. Individuals of *Pseudoceros* sp. were approximately five times as abundant as specimens of *Chromodoris preciosa*. Specimens of both species were collected by hand and were transferred to the laboratory at the Christensen Research Institute where they were maintained in 90 litre aquaria. Experimental subjects for predation experiments were conducted by collecting single individuals of four species of common reef fishes from the Christensen Research Institute dock at Nagada Harbour, Madang. Fish were collected from Nagada Harbour rather than from Kranket Lagoon to diminish the likelihood that individuals had previously encountered specimens of the two potential prey. Neither *Pseudoceros* sp. nor *Chromodoris preciosa* had been observed from the area where the fish were caught, despite repeated observation of nudibranch and flatworm populations at that locality. The four species of predators were the pallid triggerfish, *Sufflamen bursa* (Bloch & Schneider, 1801), the silty wrasse, *Halichoeres purpurescens* (Bloch & Schneider, 1801), Jansen's wrasse, *Thalassoma jansenii* (Bleeker, 1856) and the honeycomb cod, *Epinephelus merra* Bloch, 1793. All of these species are generalists that feed on a variety of small benthic prey. These fish were collected by hook and line and transferred to marine aquaria and were allowed to acclimate to laboratory conditions for 2-3 days. During the predation experiments, individual fish were isolated in the aquaria to which they had been acclimated. Polyclad or nudibranch prey were placed into the top of each aquarium by emptying a small volume of seawater containing the individual potential prey. Fish behavior was then recorded and nudibranchs and polyclads that were not consumed after five minutes were then removed to their storage aquaria. Fish were then fed small pieces of squid or bread and were not fed again until the following day's experiments had been completed. The same individual fish were then utilized for the subsequent days'experiments.

RESULTS

Evolution of aposematic coloration:

Various lineages of opisthobranchs appear to have evolved representatives that exhibit aposematic coloration. For example, the majority of sacoglossan opisthobranch clades contain animals with greenish coloration and are clearly associated with and cryptic upon specific algal prey (JENSEN, 1997). Most basal lineages contain taxa that are exclusively whitish or green in color. Some representatives of sacoglossan clades have bright, colorful pigment that is in striking contrast to that of their algal prey. For example, *Cyerce nigricans* (PEASE, 1866) is black with bright orange and blue iridescent markings that clearly make it stand out from its grassy green algal prey, *Chlorodesmis fastigiata*. A few sacoglossans within the Limapontiidae are brightly colored in contrast to their prey. Most Plakobranchidae have a greenish body color and often have contrasting parapodial margins. Within *Thuridilla* Bergh, 1872, a few species have a greenish body color while most others have brightly colored bodies with bright iridescent pigment spots and parapodial marginal lines (GOSLINER, 1995). Behaviorally, individuals of different species of *Thuridilla* are often seen crawling out in the open on shallow patch reefs. Rather than feeding on relatively large fleshy algae as is most common for species of *Elysia* Risso, 1818 (JENSEN, *op. cit.*), species of *Thuridilla* appear to feed upon small clumps of finely filamentous algae (GAVAGNIN *et al.*, 1994). Phylogenetic studies of *Thuridilla* indicate that all basal species have a green body color, while the majority of derived taxa have a bright, iridescent body. The construction of the phylogenetic hypothesis for *Thuridilla* included color characters (GOSLINER, *op. cit.*). Removal of these characters yielded a similar tree topology, but with less resolution. In both instances the most basal taxon was *T. carlsoni* Gosliner, 1995. This species lacks contrasting pigment spots or brightly colored parapodial marginal lines. *Thuridilla carlsoni* has a white marginal band that is somewhat contrasting, but is similar to that found in species of *Elysia*. *Thuridilla kathae* Gosliner, 1995 and *T. flavomaculata* Gosliner, 1995, are also basal taxa with green body color and white or cream marginal bands that are not strikingly contrasting on normal rocky substrates. One basal taxon, *T. multimarginata* Gosliner, 1995, has a green body color but has contrasting parapodial bands of reflective orange, blue and black lines. The only other species with green body color (*T. picta* (Verrill, 1901), *T. decorata* Heller and Thompson, 1983 and *T. indopacifica* Gosliner, 1995) all have brightly colored marginal lines. The remaining species all have brightly colored body pigment and other bright, contrasting pigment on the body, such as marginal parapodial lines or spots.

Sister species of *Thuridilla* have color patterns that are similar in appearance. For example, *T. gracilis* (Risbec, 1928) (as *T. bayeri* (Marcus, 1965) and *T. splendens* (Baba, 1949) both have dark brown to black bodies with cream longitudinal lines (GOSLINER, 1995: figs. 1a,b, e). Both species often have reflective blue pigment, but that pigment may be absent in some specimens of *T. gracilis*. *Thuridilla undula* Gosliner, 1995 and *T. lineolata* (Bergh, 1905) are sister species with a light blue body with parapodial bands of bright orange and a submarginal line of

black (GOSLINER, *op. cit.*: figs. 1d, 29a). In the former, the bands undulate while in the latter they are straight. In the species pair of *T. livida* (Baba, 1955) and *T. hoffae* Gosliner, 1995 both have a black body with an orange marginal line. In *T. livida* there is a reflective blue submarginal line while in *T. hoffae* there are blue patches (GOSLINER, *op. cit.*: figs. 1c, 16f).

The only species-level phylogeny for cephalaspidean opisthobranchs is that of the Gastropteridae (GOSLINER, 1989). Within the genus *Sagminopteron* Tokioka & Baba, 1964, the four species are subdivided into two clades, one of which contains two species with coloration that is cryptic on their prey sponges and the other two that are brightly colored on their prey. The two species with aposematic coloration, *S. psychedelicum* Carlson & Hoff, 1974 and *S. ornatum* Tokioka & Baba, 1964, have bright color patterns that are strikingly dissimilar. Species of the sister taxon, *Siphopteron* Gosliner, 1989 are all brightly colored and assumed to exhibit aposematic coloration, with the exception of the most basal Indo-Pacific taxon, *S. pohnpei* Hoff and Carlson, 1983, which blends in with a generalized background. Species of *Enotepteron* Minichev, 1967 are generally cryptic while species of *Gastropteron* Meckel in Kosse, 1813 may be either drably or brightly colored.The only species-level phylogenies of aeolidoidean nudibranchs are those for the Flabellinidae (GOSLINER & KUZIRIAN, 1990; GOSLINER & WILLAN, 1991). Construction of these phylogenies did not incorporate any data related to coloration or pigment patterns. Within the aeolidoidean taxon, Flabellinidae, basal species have a translucent white body color with a brown or red digestive gland that is visible through the transparent epithelium of the cerata. Often contrasting opaque white rings are present at or immediately proximal to the ceratal apices. Some more derived taxa, including *F. lineata* (Lovén, 1846), *F. capensis* (Thiele, 1925), *F. trilineata* (O'Donoghue, 1921) and *F. cooperi* (Cockerell, 1901) have additional opaque white lines on the dorsal and lateral sides of the body. Many more highly derived taxa have an orange or purple rather than white body color, including members of five distinct clades. The first clade contains two described species, *F. cynara* (Marcus & Marcus, 1967) and *F. iodinea* (Cooper, 1863). The second clade contains several taxa with papillate rhinophores: *F. delicata* Gosliner & Willan, 1991, *F. exoptata* Gosliner & Willan, 1991, *F. marcusorum* Gosliner & Kuzirian, 1990, *F. rubrolineata* (O'Donoghue, 1929), *F. poenicia* (Burn, 1957), *F. arveloi* Ortea & Espinosa, 1998 and *F. hammani* Gosliner, 1994. Many members of this clade also have subapical purple markings on the cerata. The third clade contains species with annulate rhinophores: *F. affinis* (Gmelin, 1791), *F. funeka* Gosliner & Griffiths, 1981 and *F. ischitana* Hirano & Thompson, 1990. In the cases of *F. pedata* (Montagu, 1815) and *F. rubropurpurata* Gosliner & Willan, 1991, they are the only members of their respective clades with a purple body color. Members of one subclade of *Flabellina* Voigt, 1834 containing four species all have opaque white markings on the translucent white body and cerata. In these species there is a subapical band of brightly colored pigment. However, the color patterns of these species, all of which occur sympatrically in the Philippines, are markedly different. *Flabellina macassarana* Bergh, 1905 and *F. bicolor* (Kelaart, 1858) have diffuse white pigment scattered uniformly over the surface of the body. The cerata have an orange subapical band that is darker and more diffuse in *F. macassarana*. In contrast, *F. riwo* Gosliner & Willan, 1991, has an intricate network of opaque white on the body and a purple subapical band. *Flabellina bilas* Gosliner & Willan, 1991 has alternating opaque white mid-dorsal diamonds and red and opaque white subapical ceratal bands.The clade of nudibranchs that contains the greatest number of species is the Doridoidea. Within this large taxon are two major lineages, the Phanerobranchia and the Cryptobranchia. Cryptobranchs are the most diverse in terms of numbers of species. Many of the cryptobranchs are cryptic in their coloration while other subclades predominantly contain species that exhibit aposematic color patterns. GOSLINER & JOHNSON (1994) demonstrated that the Chromodorididae and Actinocyclidae are sister taxa. The two clades exhibit dramatically different evolutionary patterns. Members of the Actinocyclidae lack defensive glands and are exclusively cryptically colored. All species thus far studied have color patterns that closely resemble the sponges on which they feed. The entire clade contains 14 species of *Hallaxa* Eliot, 1909 and two species of *Actinocyclus* Ehrenberg, 1831. There appears to be little correlation between the color pattern and phylogeny within *Hallaxa*. It is evident that species with white body color and opaque white markings evolved on a least three separate occasions in *H. translucens* Gosliner & Johnson, 1994, *H. paulinae* Gosliner & Johnson, 1994 and *H. cryptica* Gosliner & Johnson, 1994.

In contrast to the Actinocyclidae, the chromodorids exhibit very different patterns of evolution. Virtually all species of chromodorids have defensive mantle glands located around the periphery of the mantle. The species where glands are absent appear to have secondarily lost glands rather than primitively lacked them (GOSLINER & JOHNSON, 1999). While the Actinocyclidae contains only 16 described species, their sister taxon, Chromodorididae, contains more than 600 described species. In this instance, evolution of defensive mantle glands can be considered a key innovation that has contributed to the extensive radiation and speciation that has occurred in this lineage. Almost all species within this clade exhibit aposematic color patterns. Chromodorids are among the most brightly colored of shallow-water marine organisms. Species of the chromodorid clade, *Hypselodoris* Stimpson, 1855, exhibit distinct patterns of pigmentation within different subclades (GOSLINER & JOHNSON, *op. cit.*). Construction of *Hypselodoris* phylogenetic hypotheses included color pattern data. To test the impact of these data on overall phylogenetic pattern, color data were then removed from a second series of analyses. As in the case of *Thuridilla*, tree topology was conserved, but resolution was lost. Members of the clade that is found in the Atlantic and eastern Pacific Oceans have a bluish body color while members of the their sister Indo-Pacific clade generally have a translucent white body, but exhibit far more variability. The four members of the clade restricted to the eastern Pacific all have dark blue pigment with a pattern of bright yellow spots. Other aspects of their color pattern, such as marginal bands and the presence of blue spots are more divergent between species. In some Atlantic

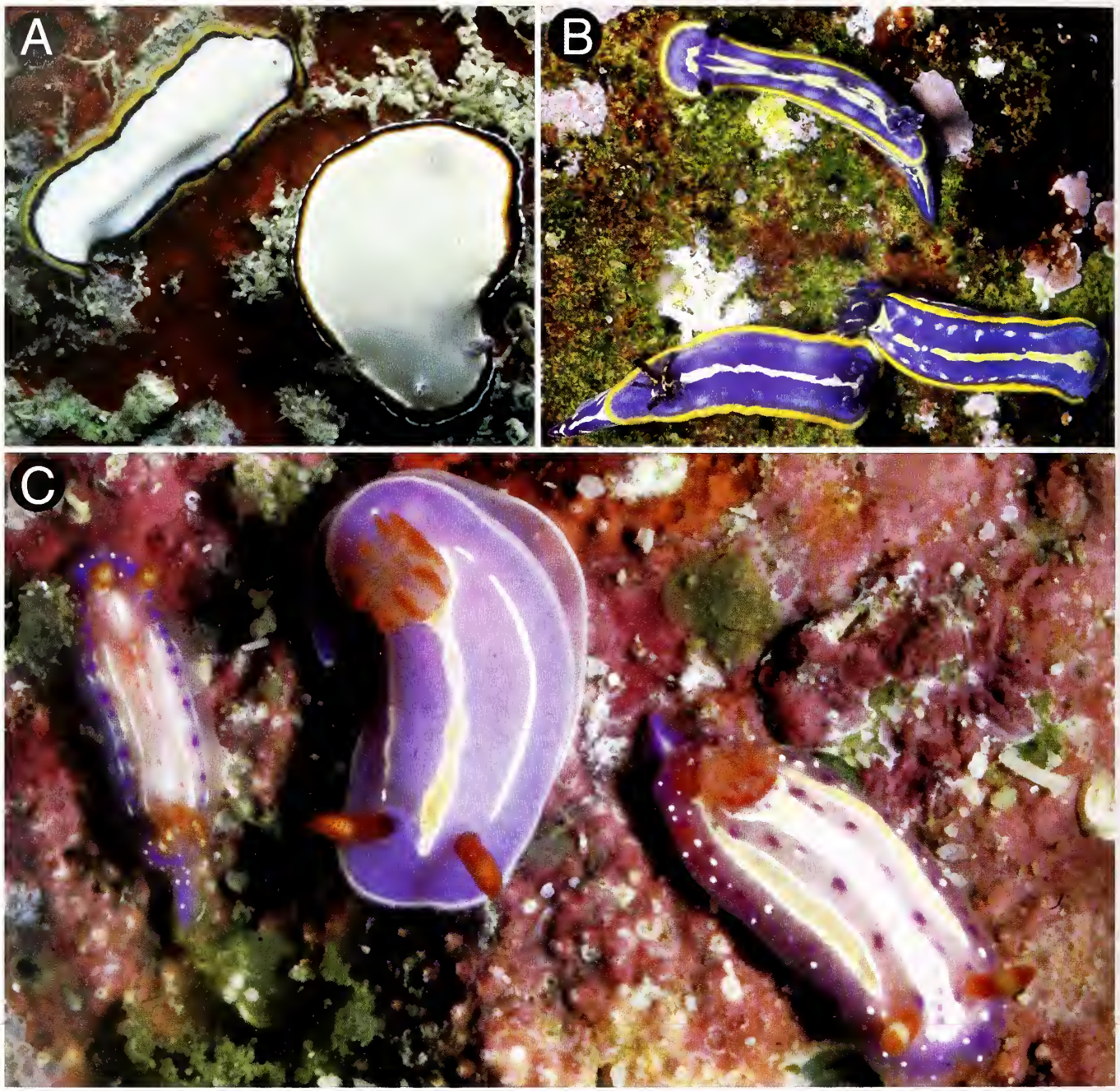

Figure 1. A. Polyclad and nudibranch mimics, left, *Pseudoceros* sp., right, *Chromodoris preciosa* (Kelaart, 1858). B. Similarly colored species of *Hypselodoris* found together at Isla Tarifa, Straight of Gibraltar, Asturias, Spain, upper, *H. bilineata* (Pruvot-Fol, 1953), lower left, *H. fontandraui* (Pruvot-Fol, 1951), lower right, *H. midatlantica* Gosliner, 1990. C. Similarly colored opisthobranchs collected within one meter of each other, southern Luzon, Philippines, left, *Hypselodoris maculosa* (Pease, 1871), middle, *Pectenodoris trilineata* (Adams & Reeve, 1850), right, *P. aurora* Johnson & Gosliner, 1998.

regions, such as the Strait of Gibraltar, as many as five or six species may be sympatric. All sympatric species share a bright blue body color with yellow lines and/or spots (Figure 1B).Within one clade of Indo-Pacific taxa, all members have a series of longitudinal lines of pigment. In the more basal members these lines are purple, while in more highly derived species the lines are opaque white. Most of the species in this clade are endemic to the Hawaiian Islands. One of these taxa, *H. alboterminata* Gosliner & Johnson, 1999, has violet lines. The remaining Hawaiian taxa that are members of this clade, *H. peasei* (Bergh, 1880) (as *H. andersoni*), *H. violabranchia* Gosliner & Johnson, 1999 and *H. insulana* Gosliner & Johnson, 1999, all have opaque white longitudinal lines. Another Hawaiian endemic, *H. bertschi* Gosliner & Johnson, 1999 is a member of another subclade of Indo-Pacific taxa. This species also has opaque white longitudinal lines despite the fact that its closest relatives lack them. The remaining two taxa found in the Hawaiian Islands, *H. infucata* (Rüppell & Leuckart, 1828) and *H. paulinae* Gosliner & Johnson, 1999 lack any hint of opaque white lines. Two white-lined sister species are also found in the western Indian Ocean. These two taxa, H. *carnea* (Bergh, 1889) and *H. capensis* (Barnard, 1927) are geographically separated. The former species is found from the Red Sea to tropical southern Africa while the latter is restricted to temperate waters of southern Africa. Sympatric with *H. carnea* in tropical southern Africa is another similarly colored species, *H. fucata* Gosliner & Johnson, 1999, which is a member of another clade. *Hypselodoris fucata* is the only member of its clade that possesses opaque white lines. The chromodorid genus *Pectenodoris* Rudman, 1984 is known from two species, *P. trilineata* (Adams & Reeve, 1850) and *P. aurora* Johnson & Gosliner, 1998. Both species are sympatric in the Philippines. *Pectenodoris trilineata* has a purple body with three longitudinal yellow or white lines. The rhinophores are uniformly red with a purple base. In contrast, *P. aurora* has a pale pink body color with purple pigment near the margins. Mid-dorsally it has three cream colored longitudinal bands surrounded by an opaque white line. There are scattered opaque white and black spots over the surface of the notum and the rhinophores are white with alternating red and white bands. The pigment pattern is very similar to that of *Hypselodoris maculosa* (Pease, 1871), which is also sympatric with the two species of *Pectenodoris*. The photo shown in Figure 1C depicts specimens of these three species all collected within a meter of each other in southern Luzon, Philippines. Members of the genus *Halgerda* Bergh, 1880 are generally brightly colored doridoideans found only in the Indo-Pacific tropics and adjacent warm temperate regions. A preliminary phylogeny of these taxa was constructed (Fahey & Gosliner, 1999) using color data in addition to anatomical characters. Subsequent analyses, removing color data, produced the same tree topology but yielded poorer resolution within some clades, as has been documented for *Thuridilla* and *Hypselodoris*. Basal taxa, such as *Halgerda dalanghita* Fahey & Gosliner, 1999 and *H. paliensis* (Bertsch & Johnson, 1982), have a more uniform and drab body color. More derived taxa have dorsal ridges that are punctuated with bright pigment that is highly contrasting with the general body color (Fahey & Gosliner, *op. cit.*). One clade, which contains species that possess distinctive reproductive anatomy, includes six species, *H. aurantiomaculata* (Allan, 1932), *H. batangas* Carlson & Hoff, 2000, *H. carlsoni* Rudman, 1978, *H. diaphana* Fahey & Gosliner, 1999, *H. malesso* Carlson & Hoff, 1993 and *H. terramtuentis* Bertsch & Johnson, 1982. All of these species have bright orange pigment on the notal ridges or tubercles and small black spots on the surface of the gills and rhinophores. Some of these may have additional secondary orange spots or lines over the surface of the dorsum.

Predator/prey feeding experiments

Feeding experiments were initially conducted with individual nudibranchs with different species of fishes. These nudibranchs were chosen because they represented different color patterns and some appeared to be cryptic in appearance while others are brightly colored. Specimens of two brightly colored dorid nudibranchs, *Chromodoris magnifica* and *C. annae*, were offered to individuals of four different species of fishes, Jansen's wrasse, a silty wrasse, a pallid triggerfish and a honeycomb cod. Neither of these nudibranchs was attacked by any of the fishes. After a period of five minutes, a specimen of the aeolid nudibranch, *Phyllodesmium briareum*, which is normally cryptic on its soft coral prey, was offered to the same predator individuals. The silty wrasse and the honeycomb cod avoided the nudibranch. The Jansen's wrasse mouthed and rejected the nudibranch. The nudibranch crawled away unharmed. The pallid triggerfish ate one specimen of *P. briareum* and regurgitated several cerata. Immediately following ingestion, the triggerfish flared its gills and opened and closed its mouth rapidly for 30-60 seconds. After approximately five minutes, it was offered a second individual of *P. briareum*. It ingested it and regurgitated several cerata. The gills and mouth exhibited the same reaction as with the first nudibranch. After another five minutes elapsed, the triggerfish was offered a third specimen of *P. briareum*. The nudibranch was closely scrutinized by the triggerfish but there was no attempt to ingest this individual. The following day, all four species were offered specimens of *Phyllodesmium briareum*. All species avoided any feeding attempts of the nudibranchs and specimens of the cryptically colored sacoglossan, *Plakobranchus* sp., but readily consumed pieces of squid and small chunks of bread. A specimen of the brightly colored aeolid, *Flabellina riwo*, was offered to all four fishes. It was avoided by all potential predators, with the exception of the pallid triggerfish. The triggerfish ingested one specimen and regurgitated it in a damaged condition. The triggerfish was offered a second specimen of *F. riwo*. It ingested the nudibranch, but immediately regurgitated it unharmed. The triggerfish avoided a third specimen of *F. riwo*. On day three, all four species of fish avoided specimens of *Phyllodesmium briareum*, but readily consumed squid and bread. No further experiments were conducted with specimens of *Plakobranchus* sp. or *Flabellina riwo*. On day 4, specimens of the polyclad flatworm, *Pseudoceros* sp., were offered to the Jansen's wrasse, the pallid triggerfish and the honeycomb cod. The wrasse and triggerfish each ingested the polyclad and immediately regurgitated it unharmed. They avoided additional flatworm speci-

mens offered to them. The honeycomb cod readily ingested the specimen of *Pseudoceros* sp. It was immediately offered three more individuals of the same species of flatworm, each of which was readily ingested. The same cod was then offered a specimen of the nudibranch, *Chromodoris preciosa*, which has a color pattern that is very similar to the polyclad. The cod readily ingested the nudibranch and rapidly regurgitated it unharmed. Its gills flared and its mouth was held open and quivering for approximately five minutes. After it appeared to recover, the cod was offered an additional specimen of the nudibranch. It avoided the nudibranch. It was subsequently offered additional specimens of the similarly colored polyclad, which it also avoided. The same cod specimen was offered the same species of polyclad and nudibranch for each of the next seven days. It avoided both potential prey on all subsequent occasions, but continued to consume squid and bread.

DISCUSSION

Color patterns in opisthobranch gastropods are varied in their evolutionary history. In many instances, the more basal members of clades are more drably colored and cryptic than the more derived taxa. Within the sacoglossan genus *Thuridilla*, more basal species have a green body color without markedly contrasting parapodial margins. More derived members of this clade have brightly colored, reflective pigment with contrasting parapodial margins. Within the cephalaspidean taxon, Gastropteridae, the subclade of *Siphopteron* found in the Indo-Pacific region, the most basal taxon is cryptically colored while the remaining, more derived species are all aposematically colored. Flabellinid aeolid nudibranchs also exhibit a pattern where more basal taxa are less brightly colored than more derived ones. More derived species have additional opaque white lines on the dorsal surface and often have brightly colored rather than translucent white bodies. More basal members of the dorid nudibranch genus *Halgerda* are cryptically colored while all derived taxa are aposematic in their color patterns. In the majority of clades studied thus far, the more derived taxa can be considered to be more brightly colored than their less derived ancestors. Unfortunately, corresponding data about the relative toxicity of these taxa are not currently available. It would not be unexpected however to find a positive correlation between increased distastefulness and greater use of aposematic coloration in more derived members of clades.

In a few cases, some clades contain only cryptically colored species while their sister taxon contains only aposematically colored representatives. One subclade of the cephalaspidean taxon *Sagaminopteron* contains two species that are aposematically colored while its sister subclade includes two species that are cryptic. Two major sister clades of cryptobranch dorids are the Actinocyclidae and Chromodorididae. The former contains all cryptic taxa while the latter includes some of the most vividly colored of all nudibranchs and virtually all members are brightly colored. These sister clades also exhibit very different patterns of adaptive radiation. The Actinocyclidae contains only 16 species worldwide, while its sister taxon has more than 600 described species. It has been hypothesized (GOSLINER & JOHNSON, 1994) that these differences in adaptive radiation and color patterns relate directly to the presence of a key innovation in the Chromodorididae, the presence of defensive mantle glands. Another general aspect of the evolution of color patterns that exhibits variation, is that closely related or sister species tend to have similar color patterns. The exception is found in closely related species of the species rich taxon, *Flabellina*, which tend to have divergent color patterns in members of the same clade. Here the pattern of opaque white pigment and color of ceratal bands varies considerably between species. Most other opisthobranch taxa that have been studied appear to have inherited elements of their color pattern from their common ancestor. In *Thuridilla*, sister species tend to have similar color patterns. This pattern is also evident for species of the aposematic dorid taxa *Hypselodoris* and *Halgerda*. The evolution of color patterns is especially well documented in *Hypselodoris* (GOSLINER & JOHNSON, 1999). In this clade there is a strong positive correlation between biogeography, phylogeny and similarity of color pattern. The two major sister groups are geographically vicariant with one occurring in the Atlantic and eastern Pacific and the other occurring only in the Indo-Pacific. Atlantic and eastern Pacific taxa all have a blue body color. Even within this clade, the eastern Pacific taxa, which represent a monophyletic subclade, all have very similar color patterns that are distinct from the Atlantic taxa.

In the Indo-Pacific subclade, there are superb examples of the relationship between evolution of a common pattern within a clade and phylogeny. Members of one clade all have opaque white longitudinal lines on the dorsal surface of the body. The most parsimonious explanation of this color pattern is that it was inherited from a single common ancestor. Sympatric with these white-lined species are additional species that have white lines. However, phylogenetic analysis indicates that these taxa are not as closely related to the white-lined species as they are to other species that lack white lines. Thus, these color patterns appear to have evolved convergently. At a single locality there may be sympatric congeneric species that have evolved similar color patterns from a common ancestor as well as others that represent cases of convergence. We also see evidence that other closely related taxa at a lower degree of relationship have examples of convergence when they are found sympatrically. Sister species of *Pectenodoris* have some elements of the same color pattern that is likely inherited from their common ancestor, but the convergence between *P. aurora* and the more distantly related *Hypselodoris maculosa* is striking. Convergent evolution is also found frequently in taxa that are far more distantly related, such as nudibranchs, flatworms and holothurians (GOSLINER & BEHRENS, 1990).

One would expect that sister species that were vicariantly separated would have similar color patterns at the time of divergence of their populations. However one would not expect these patterns to persist for long periods of time, if allopatry continues and these taxa are living outside of the context of individual predators that can learn to recognize the similarity of their color pattern. It is surprising that some of the deeply-based phylogenetic color patterns have persisted for significant

periods of time. In the absence of a fossil record, it is virtually impossible to know how old some of these clades of soft-bodied animals might be. However, some circumstantial evidence is illuminating. For example, we know that the eastern Pacific clade of *Hypselodoris* has all of its closest relatives in the Atlantic, not in other parts of the Pacific. We also know that these taxa have been isolated from their Atlantic ancestors since the closure of the Isthmus of Panama some 3.5 million years ago. Yet, the basic blue body with yellow pigment has persisted in the eastern Pacific members of the clade. There have been some modifications in the pattern in that the blue is darker and the yellow is in the form of spots rather than lines in all Pacific members of this clade.

Feeding experiments on various nudibranchs and polyclads by different predators demonstrate several consistent behavioral patterns. Most "naïve" fish that are generalists on varied small benthic prey attempted to feed on nudibranchs when they were offered. Most fishes regurgitated the nudibranchs or portions of the body in the case of some cerata-bearing nudibranchs. Generally, these encounters left the nudibranch unharmed. This fact suggests that individual selection is strongly favored as an explanation for the evolution of aposematic coloration rather than having to invoke group selection models, which have been strongly criticized (Rosemberg, 1989; Tullrot & Sundberg, 1991). Wiklund & Jarvi (1982) have suggested individual selection as the primary method of adaptation for aposematically colored insects that survive attacks by birds. Another conclusion from the feeding experiments is that predators learn rapidly to associate unpleasant encounters of attempting to feed on nudibranchs with the specific color patterns exhibited by the particular slug species. The learning experience and subsequent avoidance of nudibranch prey persisted for at least the entire time that the experiments were conducted, which in one instance was up to a week in duration.

Other conclusions about the evolution of mimicry can be drawn from the experiments involving similarly colored specimens of the polyclad flatworm, *Pseudoceros* sp., and *Chromodoris preciosa*. In two cases the predators regurgitated specimens of the polyclad and avoided the nudibranchs. The third species of fish, the honeycomb cod, readily ate the polyclads but rejected the nudibranch. Subsequently, the fish avoided both the nudibranchs and the polyclads. This suggests a classic Batesian mimicry scenario where the model (*C. preciosa*) is unpalatable and the mimic (*Pseudoceros* sp.) is palatable. A complicating factor to this hypothesis is that the mimic is found in greater densities in the natural habitat than the model. One possible explanation of how this mimicry can be stable stems from the fact that the polyclad is also unpalatable to two of the three remaining fish tested. This suggests that in the case of multiple predators, these two potential prey species actually represent cases of Müllerian mimicry, since both are likely to be unpalatable. The situation occurring with *Pseudoceros* sp. and *Chromodoris* sp. blurs the distinction between the classification of similarly colored taxa as strictly Batesian or Müllerian mimics. If the distinction is species-specific for different predators found sympatrically, it is suggestive that differences in relative palatability vary on a continuous gradient rather than as absolutes.

Evolution of aposematic color patterns in opisthobranchs exhibits generalized patterns of becoming more prevalent and more overtly manifested in more derived rather than more basal taxa. Sympatric species with similar color patterns exist as products of both inheritance from a common ancestor as well as from convergent evolution. Utilization of contemporary phylogenetic analytical methods permits the distinction of color pattern evolution between common descent and homoplasy. Species-specific differences in palatability for different predators of similarly colored species complexes blur traditional distinctions between Batesian and Müllerian mimicry. Future studies on evolution of color patterns and mimicry in opisthobranchs should correlate these findings with chemical data and other tests for toxicity and relative palatability. This exercise will provide valuable data for determining whether more brightly colored species are in fact more distasteful to predators.

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Taxonomical and ecological aspects of the nudibranch *Geitodoris patagonica* Odhner, 1926 (Opisthobranchia, Doridina) from Argentina

Claudia Muniain

KEY WORDS: Gastropoda Nudibranchia, *Geitodoris patagonica*, taxonomy, redescription, chemical ecology, Argentina.

ABSTRACT *Geitodoris patagonica* Odhner, 1926 is redescribed based on the study of numerous specimens collected from Patagonia (Argentina). The external coloration, radular morphology and reproductive system are examined. The defensive behaviour is investigated comparing it to the mechanical and chemical strategies recently found in other Magellanic dorid nudibranchs. The record of *G. pusae* (Marcus, 1955) from Argentina, and the synonymy of *G. patagonica* with G. *falklandica* Odhner, 1926 are discussed. The taxonomical and ecological results are discussed and compared to other *Geitodoris* species, principally those present in the Atlantic Ocean..

RIASSUNTO *Geitodoris patagonica* Odhner, 1926 viene ridescritta in base allo studio di numerosi esemplari raccolti in Patagonia (Argentina), esaminando la colorazione esterna, la morfologia radulare ed il sistema riproduttivo.
Il comportamento difensivo viene studiato confrontandolo con le strategie meccaniche e chimiche messe in atto da altri doridacei magellanici.
I risultati tassonomici ed ecologici sono confrontati e discussi con quelli relativi alle altre specie di *Geitodoris*, soprattutto quelle presenti nelle acque atlantiche. .

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INTRODUCTION

The genus *Geitodoris* Bergh, 1891 was created for species whose lacking a differentiated prostate and having two types of lateral teeth, the inner ones hooked and the outer ones spatulated. Recently, MILLER (1996) described a new species of *Geitodoris* from New Zealand, reviewing the classification of the genus and clarifying the relationships with the genus *Discodoris* Bergh, 1877.

The nudibranch *Geitodoris patagonica* was described by ODHNER (1926) from Puerto Madryn (Chubut, Argentina) and has not been redescribed since its original description. Several authors (CARCELLES, 1950; CARCELLES & WILLIAMSON, 1951; CASTELLANOS, 1970; ORTEA & BALLESTEROS, 1981; PERRONE, 1992; MILLER, 1996) considered this species as valid, within the genus *Geitodoris* from the Western Atlantic. However, these authors did not examined the type material or newly collected specimens.

Three species belonging to the genus *Geitodoris* Bergh, 1891 have been recorded from the South Atlantic: *G. patagonica* Odhner, 1926 (from Patagonia, Argentina); *G. falklandica* Odhner, 1926 (from the Falklands Islands) and *G. pusae* (= *Discodoris pusae* Marcus, 1955) (from Florida to Argentina 40° 56'S). The species *Discodoris pusae* was transferred to *Geitodoris* and considered as an amphiatlantic species by ORTEA & BALLESTEROS (1981), and ORTEA, LUQUE & TEMPLADO (1988).

Following the studies on defensive behaviour recently investigated in Magellanic opisthobranchs (MUNIAIN, 1997; FONTANA ET AL, 1998; GAVAGNIN ET AL, 1999; MUNIAIN ET AL, 1999), the mechanic and chemical defensive strategies found in Magellanic dorid nudibranchs are compared to those present in *G. patagonica*.

The present paper contributes to the taxonomic redescription of this species, based on living animals, and new results on ecological aspects of *Geitodoris patagonica* from Argentina.

MATERIAL AND METHODS

Since 1991, numerous specimens of *G. patagonica* have been collected from Patagonian localities (Argentina), in intertidal rock pools and by scuba diving (2-5 m depth). For all the specimens, the total length alive was measured, and information on the coloration, diet, reproductive behaviour, was taken. The radula, jaws and mantle (critically point dried) were examined using scanning electron microscope (SEM). In several specimens, the buccal secretions were tested with pH indicator strips (pH: 0-14) at the moment of collection. The chemical analysis was made at the Istituto per la Chimica di Molecole di Interesse Biologico (Naples, Italy), where the frozen animals were dissected. The mantle, foot and digestive gland were isolated, and extracted with acetone. Each extract was chromatographed on silica gel plates in chloroformethanol, and later checked for fluorescent compounds by exposure under UV.

A voucher specimen is deposited at Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", MACN: 34257. 1 specimen 42 mm long (Not dissected). 31 December 1994, Punta Marques (Chubut).

RESULTS

SYSTEMATICS

Suborder Doridina
Superfamily Eudoridoidea
Family Dorididae Rafinesque, 1815
Genus *Geitodoris* Bergh, 1891

Geitodoris patagonica Odhner, 1926
(Figs. 1- 5)

Geitodoris patagonica Odhner, 1926: 80-81, pl. 3, figs. 42-43; Carcelles, 1950: 70, pl. 3, fig. 56; Carcelles and Williamson, 1951: 316; Muniain, 1997: 24, fig. I 3C.

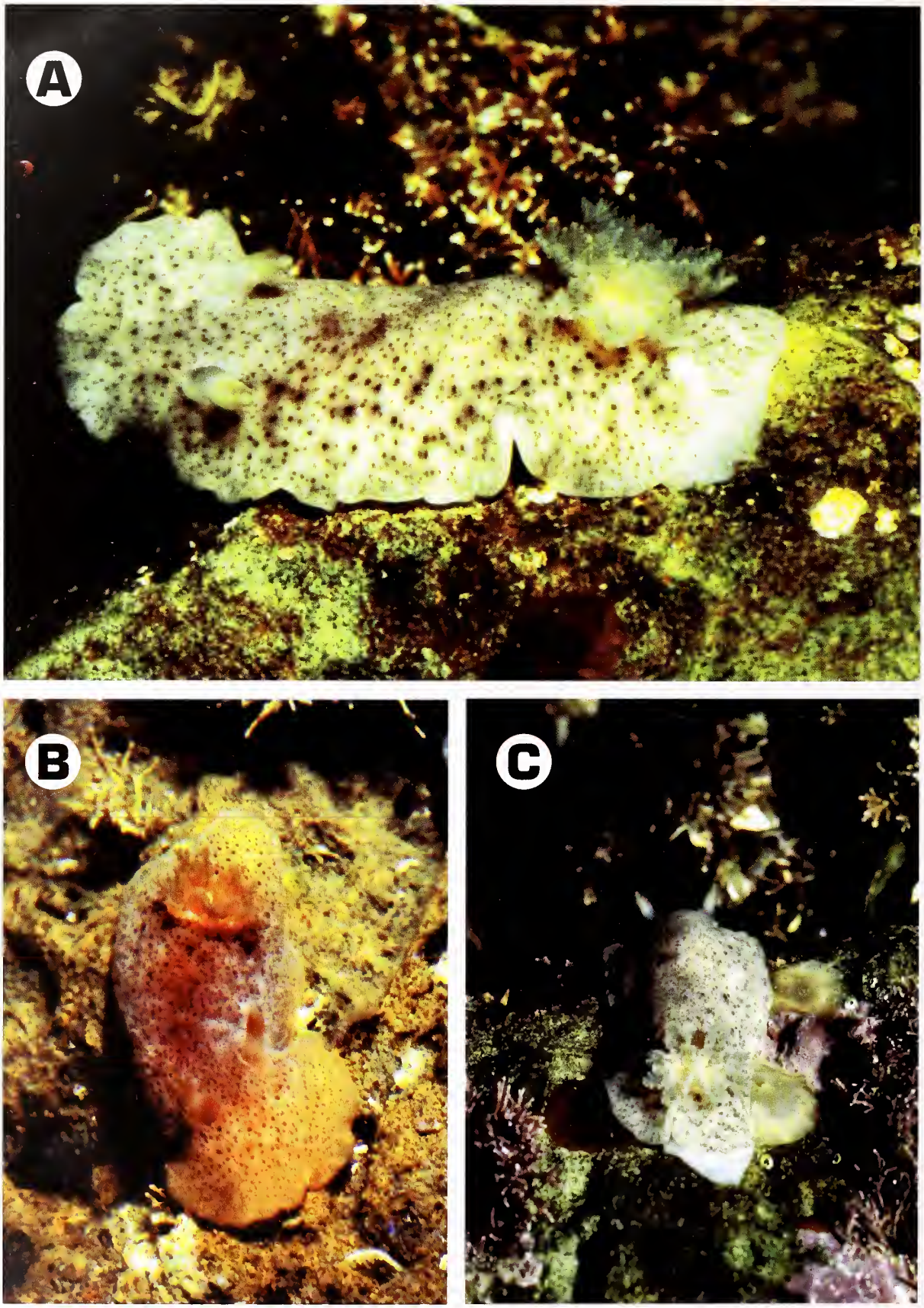

Figure 1: *Geitodoris patagonica* living animals from Rada Tilly (Chubut). Photograph by Claudia Muniain. A. Specimen showing the white pattern spotted with black dots. B. Specimen showing the yellow pattern. C. Dorsal view of the same specimen A, showimg the branchial crown and the foot extending posteriorly.

Geitodoris patagonicus (non Carcelles, 1944: 264); Castellanos, 1970: 148, pl. 11, fig. 8; Scarabino, 1977: 195, pl. 1, fig. 10.

Geitodoris falklandica Odhner, 1926: 83, pl. 3, figs. 44-46; Carcelles, 1950: 70, pl. 3, fig. 59; Carcelles and Williamson, 1951: 315; Muniain, 1997: 24.

Geographic Range: From Northern Chubut to Falklands Islands (Magellanic Province).

Type Locality: Puerto Madryn, Chubut (42° 30'S).

External morphology

Body length up to 30-50 mm. The background colour of the body varies from white, yellow-orange to dark grey, spotted with black dots on the dorsum (Fig. 1 A-C). The coloration has no relation with the animal length or state of maturity. The surface of the mantle, the border of the rhinophoral and branchial sheaths are densely covered with two sizes of low and rounded tubercles. Only, from the smallest and numerous tubercles there are spicules projecting apically in number of 6-10 (observed by SEM, Fig. 2 A-B). The rhinophores are pale to yellow-cream ending in translucent tips, perfoliate with 12 to 18 lamellae. The gill has the same colour as the dorsum, spotted with black dots. There are 6-8, bi or tripinnate branchial leaves. The anal papilla lies central within the circlet of the branchial plume. Ventrally, the foot is narrow, completely white and extends posteriorly (Fig. 1 B). The anterior border of the foot is bilabiate and notched. The head is rounded and the oral tentacles are broad.

Internal Anatomy

The radular formula is 16-20 x 12.28.0.28.12 in a 46 mm alive specimen. The innermost lateral tooth is hook shaped (Fig. 3A, D). The mid lateral teeth have a small, recurved, pointed cusp, that increases in length to the end of the row (Fig. 3B, C). The 7-10 outermost lateral teeth are spatulated and are similar in length to the mid laterals (Fig. 3B). The teeth are completely smooth, lacking denticles or a serrate border. The jaw plates are well developed showing the same regular rodlets in the each side, above and below (Fig. 4A,B).

There is a conspicuous and pigmented blood gland on the oral tube. The stomach is covered with the digestive gland (Fig. 5A). The reproductive system has a long and tubular ampulla, the spherical gametolytic gland and the seminal receptacle are situated under the long vas deferens. A yellowish and elongated prostate is present. The penis is conical and unarmed. The vagina is long and narrow, a vaginal gland is present (Fig. 5B)

Ecology

Three different patterns of background coloration, spotted with black dots, were found: orange-yellow, grey-dark and white. This seems to be related to the substratum in which each specimen was lying (sponges, dark or light rocks). This defensive mechanism in which the animal resembles the uniform coloration of its background is named as crypsis: homochromy (Ros, 1976; Todd, 1981).

Part of the specimens collected were removed and frozen as soon as possible after collection, and some of them were disturbed to obtain defensive secretions. The secretions were tested with pH indicator strips, showing acid secretion (pH: 0-1).

In other biochemical studies of Magellanic nudibranchs that we have recently recorded and investigated from Argentina (Muniain et al, 1996; Muniain, 1997), we found that the species *Tyrinna nobilis* contains a number of terpenoids, obtained from the diet and stored in the mantle dermal formations (MDFs) and, in the species *Anisodoris fontainii* a series of diacylglycerols were isolated from their mantle. These natural products, as secondary metabolites, are supposed to play a defensive role in these species (Fontana et al, 1998; Gavagnin et al, 1999; Muniain et al, 1999).

Geitodoris patagonica lives in the same habitat and eats sponges as the species mentioned above, but no evidence of active metabolites has been found in the extract from the digestive gland, mantle and secretions. On the contrary, the inorganic acid secretions from the mucus has only been found in this species. Three defensive mechanisms are probable presents in *G. patagonica*: mechanical (homocromy and endoskeletal calcareous spicules) and chemical strategies (inorganic acid secretions).

DISCUSSION

The present work does not take into consideration the division of the genus *Geitodoris* into three subgenera by Ortea & Ballesteros (1981), because the species *G. patagonica* and *G. faklandica* have not been included in the list of the species studied, and a complete phylogenetic analysis clarifying this matter is necessary. The family is enumerated in order of the classification followed by Rudman & Willan (1998).

Odhner (1926), distinguished *G. patagonica* and *G. falklandica*, based on the external coloration, the morphology and number of radular teeth, the mantle tubercles and the skin porosity. The present study shows that there is a large variation in the external coloration, therefore this is not a good comparative character. The same occurs with the porosity of the mantle, which it is probably related to the different temperature conditions. There are no significant differences between the reproductive system and radula mentioned in the original descriptions of these two species, therefore these species should be considered synonyms, and the geographic range of *G. patagonica* extended to the Falkland Islands.

Unfortunately, a great confusion has existed on the records of the opisthobranchs from Argentina, where most identifications were made based on reviews of the original descriptions, without a revision of the types or comparative material (Carcelles, 1950; Carcelles y Williamson, 1951; Castellanos, 1970).

Muniain (1997) discussed the record of *Geitodoris patagonica* from the Argentinean Province stated by Carcelles (1944: 264, *as G. patagonicus*), who doubtfully assigned to this species a specimen collected from Puerto Quequén (Buenos Aires), and which did not fit to the original description and figure given by Odhner (1926). Surprisingly, my own examination of Carcelles's specimen (MACN: 18505) demonstrated that it is actually an aeolid nudibranch (incorrectly assigned or mislabelling?). Therefore, I suggest that *G. patagonica* has not been recorded from that latitude, and so far, its geographic range is restricted to the Magellanic Province.

Scarabino V. (1977) assigned to *Geitodoris patagonica* (as *G. patagonicus*) the specimens collected at 36 and 90 m depth in Golfo San Matías. It is impossible to confirm the validity of this record because there is no material deposited or description of the specimens, and the drawing included is to confusing (Scarabino, 1977: pl. 1, fig. 10).

Muniain (1997) cited and included a colour photograph of *G.*

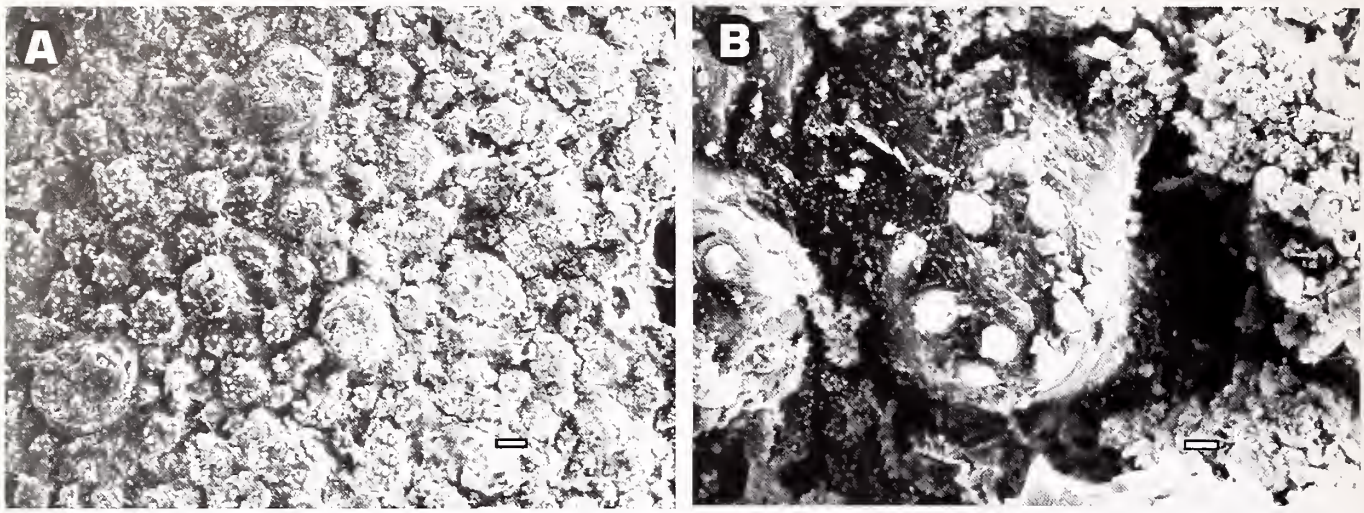

Figure 2: *Geitodoris patagonica*, scanning electron micrographs. Mantle. A. Low-magnification view of mantle tubercles. Scale bar: 100 µm. B. Detail of a single tubercle with apically projecting spicules. Scale bar: 10 µm.

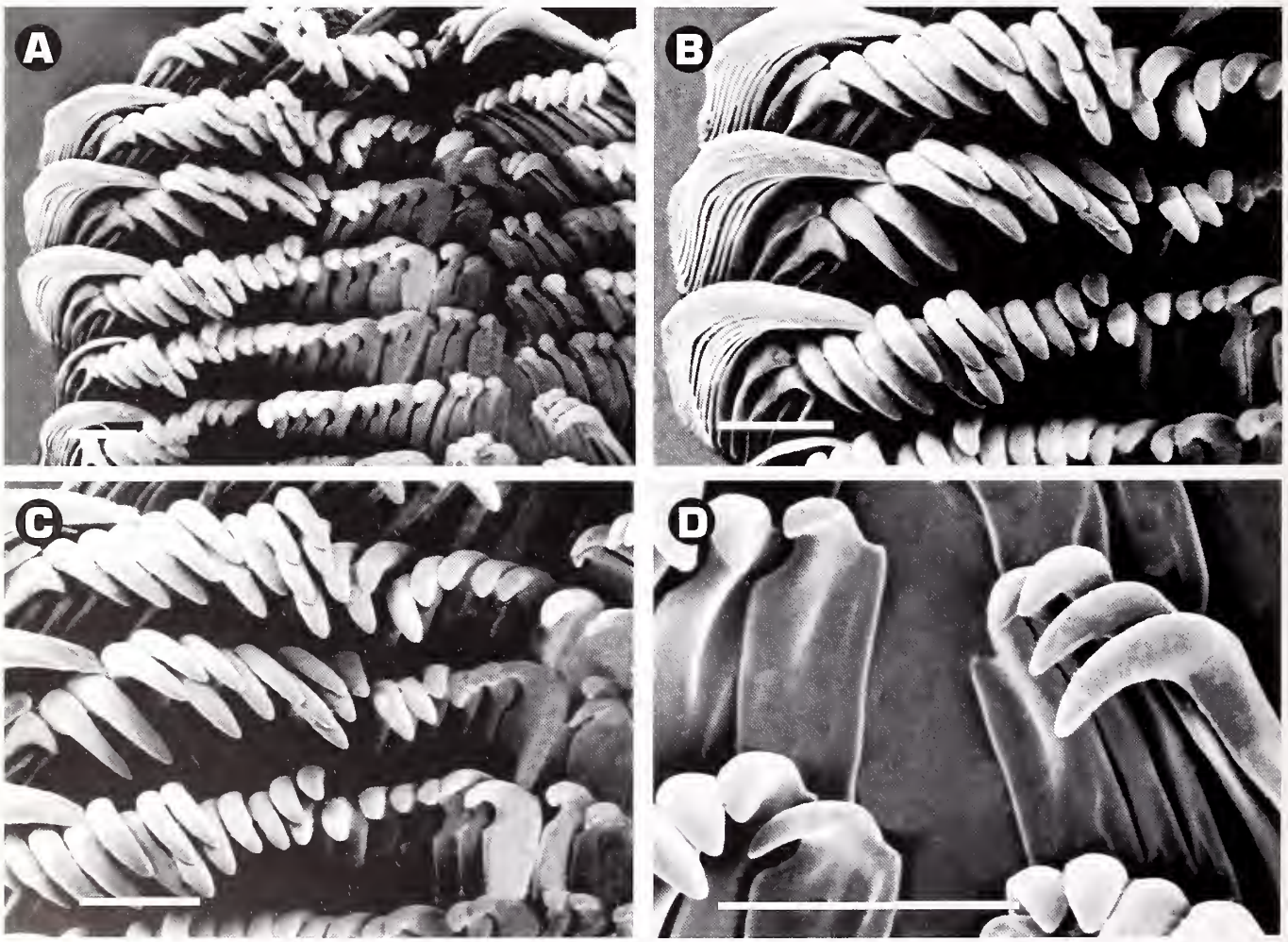

Figure 3: *Geitodoris patagonica* scanning electron micrographs. Radula. A. Half row of radular teeth. B. Outermost spatulated teeth and mid lateral teeth. C. Mid lateral teeth bearing recurved pointed cusp. D. Detail of the innermost hooked lateral teeth. Scale bar: 100 µm.

patagonica from Chubut and the distribution for this species was extended to northern Santa Cruz.

The record of the amphiatlantic species *Geitodoris pusae* Marcus, 1955 by MARCUS & MARCUS (1969), from Northern Argentina, seems to be valid, considering as consistent and separable characters of this species the presence of a reticulate mantle and the spicules in the external duct of the vestibular gland (see MARCUS & MARCUS, 1969; ORTEA ET AL, 1988; Fig. 9).

The other Atlantic species of *Geitodoris,* such as *Geitodoris planata* (Alder & Hancock, 1846), *G. reticulata* Eliot, 1906, *G. bonosi* Ortea & Ballesteros, 1981, *G. perfossa* Ortea, 1990, and *G. bacalladoi* Ortea, 1990, are clearly distinguishable from *G. patagonica* by the distribution of the spotted black dots, radular and jaw morphology, serrated border teeth, and the presence of reticulated or spherical calcareous structures on the mantle (ORTEA & BALLESTEROS, 1981; CERVERA ET AL, 1985; ORTEA, 1990; MARTÍNEZ ET AL, 1996).

Acid defensive secretions are common among opisthobranchs, and particularly in dorid nudibranchs (THOMPSON, 1960; EDMUNDS, 1968; TODD, 1981). ÁVILA (1995) compiled a catalogue of natural products and secretions in species of opisthobranch. According to this study, the absence of secondary metabolites and the presence of acid secretion (inorganic acids) in *Geitodoris patagonica* also occurs in the species *Geitodoris portmanni*; *Discodoris heathi*; *D. palma*; *D. pusae*, *D. stellifera and D. tema.* Once again, there is a close relationship between species of *Geitodoris* and *Discodoris.* See the revision by Miller (1996) about the morphological similarities into these genera..

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ADDENDUM

While this manuscript was in press, the paper by Schrödl (2000) entitled "Revision of dorid Nudibranchia collected during the French Cape Horn Expedition in 1882-1883, with discussion of the genus *Geitodoris* Bergh, 1891" was published in The Veliger 43: 197-209. In this paper, the species *Geitodoris patagonica* is revised taxonomically.

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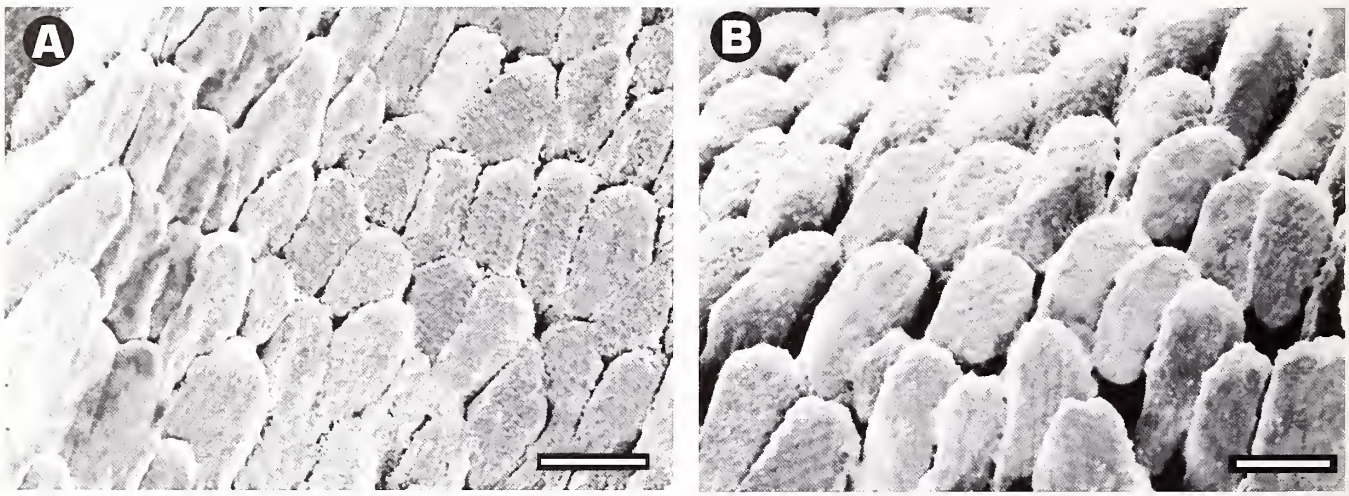

Figure 4: *Geitodoris patagonica*,scanning electron micrographs. Jaws. A. Labial rodlets, group of the right above side. B. Labial rodlets, group of the right below side. Scale bar: 20 µm.

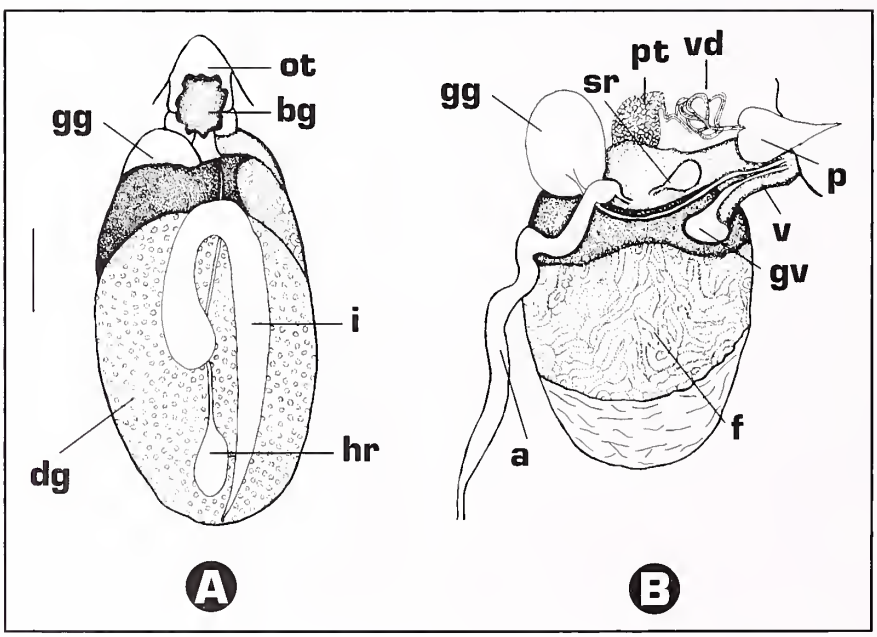

Figure 5: *Geitodoris patagonica*, A. Internal anatomy. B. Reproductive system. Abbreviations: a: ampulla, bg: blood gland, dg: digestive gland, f: female glandular mass, gg: gametolytic gland, gv: vaginal gland, hr: heart, i: intestine, ot: oral tube, p: penis, pt: prostate, sr: seminal receptacle, v: vagina, vd: vas deferens. Scale bar: 2 mm

Feeding habits of *Calma glaucoides* (Alder & Hancock, 1854): its adaptive structures and behaviour

Gonçalo Calado [1,2] *& Victoriano Urgorri* [2]

KEY WORDS: Aeolidacea; *Calma glaucoides*; Feeding

ABSTRACT *Calma glaucoides* (Alder & Hancock, 1854) is an aeolid nudibranch inhabiting European (Atlantic and Mediterranean) Western and Southern coasts. Adults feed on fish eggs, thus being found near spawning sites on the underside of boulders or in small crevices, where male fish nest. This aeolid has an atypical uniseriate radula. Little is known about formation or function of this radula, but it is believed that such a peculiar morphology is related to adult's feeding habits. The feeding behaviour of individuals could be observed in aquaria. It was also possible to study not only radulae from individuals of different sizes but also the damage caused by radula action upon fish egg membranes. These were visible under SEM after critical point drying of empty eggs. SEM images suggest that the radula is used as a saw. After the egg is "opened" the yolk and embryo are sucked out with the help of strong buccal musculature, leaving the external membrane of the egg almost intact. The way these animals puncture fish eggs, associated with the early development of their radula, lead us to conclude, that there seems to be no food size constraint, as previously had been thought.

RIASSUNTO *Calma glaucoides* (Alder & Hancock, 1854) è un eolidiaceo presente lungo le coste dell'Atlantico occidentale e del mediterraneo. L'adulto si nutre di uova di pesci e viene spesso ritrovato vicino alle ovature, sul lato inferiore dei massi o in piccole fessure della roccia. Questo eolidiaceo ha una radula uniseriata molto atipica. Poco conosciute sono la sua formazione e funzione, ma si pensa che la tipica morfologia debba essere correlata al comportamento trofico della specie. Grazie al mantenimento di alcuni esemplari in acquario, è stato possibile studiare il comportamento di questa specie, la morfologia radulare in individui di diversa taglia e i danni causati dalla radula stessa sulla membrana delle uova dei pesci. Immagini al SEM, dopo il critical point, delle uova indicano che la radula viene usata come una sega. Dopo che l'uovo è stato tagliato, il tuorlo e l'embrione vengono risucchiati grazie all'azione di una forte muscolatura, lasciando praticamente intatta la membrana esterna dell'uovo. Il modo con cui questi nudibranchi tagliano le uova, in rapporto anche al primo sviluppo della radula, suggerisce che la taglia dell euova non sia un fattore limitante, come precedentemente supposto.

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INTRODUCTION

Most aeolid nudibranchs feed on cnidarians and therefore they possess strong jaws and uniseriate or triseriate radulae, with few exceptions in both characteristics. *Calma glaucoides* (Alder & Hancock, 1854), an aeolid nudibranch inhabiting European (Atlantic and Mediterranean) Western and Southern coasts, is precisely one such exception. Adults (7 to 18 mm) are found on their food supply, the spawn of teleost fishes such as *Lepadogaster lepadogaster*, *Lepadogaster candollei*, *Parablennius gattorugine* and *Parablennius pilicornis,* which deposit their eggs on the underside of boulders or empty bivalve shells. *C. glaucoides* has a very atypical "uniseriate" radula, previously described as a row of very small teeth and a group of few bigger teeth at the distal end. Little is known about the formation or function of this radula, but it is believed that such a peculiar morphology is related with adult's feeding habits (Evans, 1922; Rowett, 1946). The extent of such a relation is the subject matter of this study.

MATERIALS AND METHODS

We worked with specimens obtained from the Iberian Atlantic Coast (Galicia – NW Spain (43° 27' N, 8° 16' W) and Arrábida, Portugal (38° 27' N, 9° 0' W)). They were preserved in 70% ethanol. Buccal masses were extracted and placed in a 5% NaOH solution for 24 h at 40° C. When radulae were detached they were abundantly rinsed in tap water. Six radulae for SEM were dried and coated with gold prior to examination.

In order to observe their feeding behaviour, three recently collected individuals of *C. glaucoides* were kept in small beakers with small stones containing portions of *Parablennius pilicornis* spawn. After consumption of the egg contents, empty egg membranes were dehydrated in alcohol, and observed in SEM after critical point treatment.

RESULTS

Radular morphology

SEM images allowed a closer examination of seemingly important details. Small teeth of the serration measure about 1mm (Fig. 1) and in high magnification (top image) it is possible to see some erosion on their outer edges (Fig. 2). In small animals, the first-formed "big" teeth were smaller than in later ones, as if they were in formation after differentiation of the distal edges. Radula size differs relating little between animals having a body length of 1.4 mm from those of 2.5 mm (Fig. 3). This suggests that the radular morphology, developed early in the ontogeny, is preserved throughout adult life. Similar arrested morphological development of the radula is known, for example, from the Harpidae (Hughes & Emerson, 1987).

Feeding behaviour

In order to consume an egg, *Calma glaucoides* crawls over the fish spawn. Then it proceeds to enwrap an egg with its oral tentacles; immediately afterwards we can see, through the almost transparent body, the egg contents being sucked in and rapidly moved along the oesophagus to the stomach. During the feeding process,

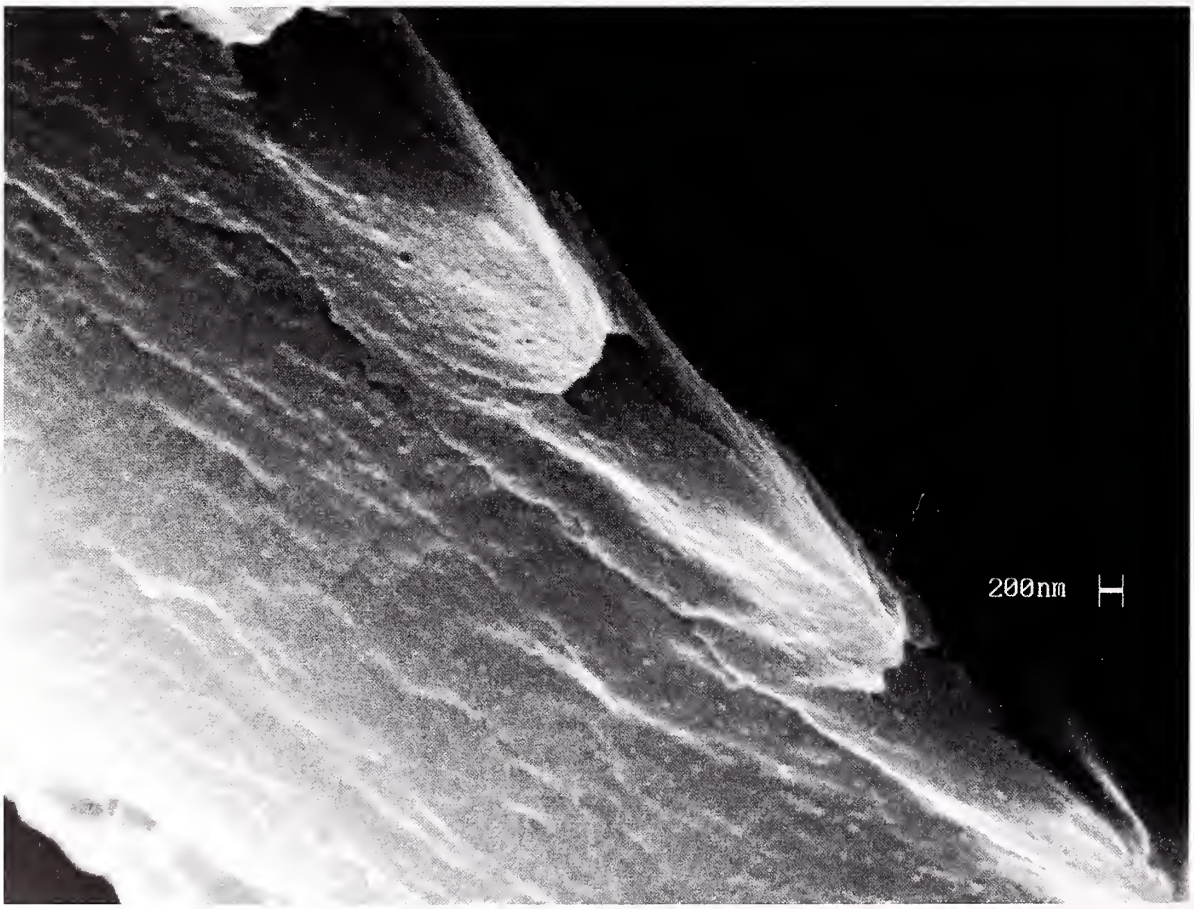

Fig. 1 - SEM picture of a radula where saw-like teeth are visible.
Fig. 2 – Top image of serrated bar with saw-like teeth.

Fig. 3 - SEM views of two radulae. Left: from a 1.4 mm long specimen. Right: from a 2.5 mm long specimen. Scale bar for both pictures.
Fig. 4 – Predated *Parablennius pilicornis* eggs.

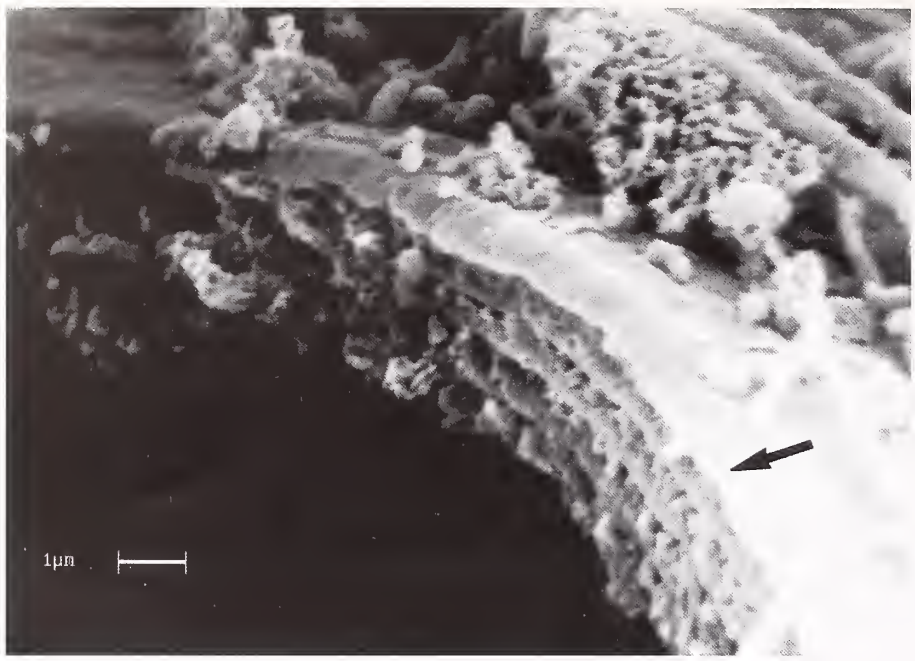

Fig. 5 - Detail of the incision in the egg membrane. Arrow indicates outer border.

immediately before suction the animal usually bends forwards all its cerata, letting them return to the "normal" position after the actual suction begins. The opening of the egg membrane was observed to be a quick task. If by any chance the egg already contains an embryo, it is apparently crushed during suction process, as we see it into small pieces. The procedure above is repeated with a succession of eggs, until the animal is satiated, leaving behind a variable band of empty egg membranes. Under laboratory conditions we observed up to 30 eggs being continuously consumed, in less than one hour, by a single adult individual.

SEM images of empty fish egg membranes (figs. 4 and 5) allow us to see the size and shape of the opening made by the mollusc. It clearly shows evidence of radular action as discussed below.

DISCUSSION

Erosion on the outer border of teeth, on the serrated portion of the radula, made us believe that these teeth are functional, regardless of their small size (as compared with those of other aeolidaceans). Examination of fish egg membranes after consumption seems to agree with this view. Moreover, there is a reduced radula size difference between animals having a markedly different body length, making us suspect that the entire "adult-like" radular morphology is developed early in the ontogenetic process. In fact we have observed smaller animals feeding in a manner similar to larger ones.

Therefore, one can assume that juveniles already feed on fish eggs, contrarily to the previous assumption that juveniles are general carnivores (EVANS, 1922). Thus, there seems to be no food size constraint.

Terminal larger teeth seem to continue differentiating, from the juvenile phase onwards, making us believe that they may also be useful for the adult's feeding behaviour. EVANS (1922) suggested that these teeth might be used only in the post-settlement phase, before juveniles could find fish spawn.

SEM images of empty fish egg membranes show openings, made by the molluscs, that are consistently regular as if cut with a "surgical" instrument and not just torn open. The openings observed were morphologically identical and suggest a sawing-like method of cutting, precise and efficient. The observation of living animals while feeding also indicates that this procedure is a rapid one. We conclude that the saw-like portion of the radular tooth is used to cut open the membrane with a minimum effort allowing its inner content (which may contain hard parts, if fish's larva is already formed) to be extracted.

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South American Opisthobranchia (*Mollusca: Gastropoda*) collected by Charles Darwin during the "Beagle" expedition in 1832-1835

Michael Schrödl

KEY WORDS: Charles Darwin, Opisthobranchia, Nudibranchia, Magellanic region

ABSTRACT CHARLES DARWIN collected a number of opisthobranch molluscs from Magellanic waters and briefly described them within the "Zoology Notes", a collection of hand-written field notes. None of these species, roughly called "Doris", "Cavolina", "nudibranch", or "Pleurobranchus", were either identified or named by DARWIN; museum material could not be traced. However, my recent, comprehensive taxonomic review of Chilean opisthobranchs paired with Prof. KEYNES' (Cambridge) first public edition of the Zoology Notes now provide the faunistic and descriptive background needed to interprete DARWIN's notes. While some descriptions are very rudimentary, others give surprisingly detailed morphological and biological information. The present study identifies five of DARWIN's Magellanic opisthobranchs to species level, i.e. the pleurobranchid *Berthella platei* Bergh, 1898, the common aeolid *Phidiana lottini* (Lesson, 1831) and the doridoidean nudibranchs *Anisodoris fontaini* (d'Orbigny, 1837), and *Anisodoris punctuolata* (d'Orbigny, 1837). *Thecacera darwini* Pruvot-Fol, 1950, a species which was named in honour of a southern Chilean polycerid collected by DARWIN is confirmed to really refer to the "nudibranch coming nearest to Scyllaea" from Cerro Tres Montes which was described accurately by DARWIN more than a century before.

RIASSUNTO CHARLES DARWIN raccolse un certo numero di molluschi opistobranchi nell'area magellanica, descrivendoli nelle "Zoology Notes", una raccolta manoscritta di osservazioni di campo. Nove di queste specie, grossolanamente chiamate "Doris", "Cavolina", "nudibranch" o "Pleurobranchus", non furono mai descritte dallo stesso DARWIN nè è stato possibile rintracciarle in collezioni museali. Le recente review sui molluschi opistobranchi del Cile e la recente pubblicazione delle "Zoology Notes" a cura del Prof. R.D. KEYNES (Cambridge) hanno permesso di interpretare le osservacioni di DARWIN. Mentre alcune note sono molto superficiali, altre danno dettagliate informazioni sia morfologiche che biologiche. Il presente studio permette di identificare, a livello specifico, 5 specie osservate da DARWIN nell'area magellanica: *Berthella platei* Bergh, 1898, il comune eolide *Phidiana lottini* (Lesson, 1831) e i doredacei *Anisodoris fontaini* (d'Orbigny, 1837) e *Anisodoris punctuolata* (d'Orbigny, 1837). Viene infine confermato che *Thecacera darwini* Pruvot-Fol, 1950 è realmente riferibile a "nudibranch coming nearest to Scyllaea", un policeride raccolto e descritto con accuratezza da DARWIN píu di cent'anni prima della descrizione originale.

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INTRODUCTION

During the famous "Beagle" Cruise, DARWIN collected an enormous variety of marine organisms. He documented his findings within the "Zoology Notes", a collection of hand-written field notes. The first public version of the "Zoology Notes" edited and commented on by Prof. KEYNES (in press) presents live descriptions of several opisthobranch molluscs from South America: one polycerid doridoidean which was mentioned as "Nudibranch allied to Scyllaea?", one aeolid "Cavolina" and some "Aplysia" from Brazil, but most species were collected from Magellanic waters, i.e. from the Falkland Islands, Tierra del Fuego and Chiloé Island, southern Chile. None of these species, roughly called "Doris", "Cavolina" "nudibranch" or "Pleurobranchus", was identified or named by DARWIN. At that time only two nudibranch species were known from temperate waters of South America: the doridoidean *Doris amarilla* Pöppig, 1829, which was not adequately described for reidentification (SCHRÖDL, 1996), and the aeolidoidean *Phidiana lottini* (Lesson, 1831) which recently (see SCHRÖDL, 1996, 1997b) was considered to be a senior synonym of the well-known *Phidiana inca* (d'Orbigny, 1837). More significant faunistic contributions were published later, i.e. those of D'ORBIGNY (1835-1846; "Voyage dans l'Amerique Méridionale"), GOULD (1852, 1856; "United States Exploring Expedition"), ABRAHAM (1877), and ROCHEBRUNE & MABILLE (1891; "Mission Scientifique du Cap Horn"), however, all just provided external, sometimes very sketchy descriptions. Later workers such as BERGH (1884, 1894, 1898), ELIOT (1907), ODHNER (1926), MARCUS (1959), and MARCUS & MARCUS (1969) added anatomical data on many species but sparse information on living specimens. Just recently, external descriptions of living Chilean opisthobranchs and detailed taxonomic revisions (e.g. SCHRÖDL, 1996, 1997a,c, 1999, 2000a,b), paired with Prof. KEYNES' edition of the Zoology Notes (KEYNES, in press), allow to interprete DARWIN's notes.

MATERIAL AND METHODS

Text in quotation marks refers to DARWIN's (CD) original notes which were taken from Prof. KEYNES' edition of the

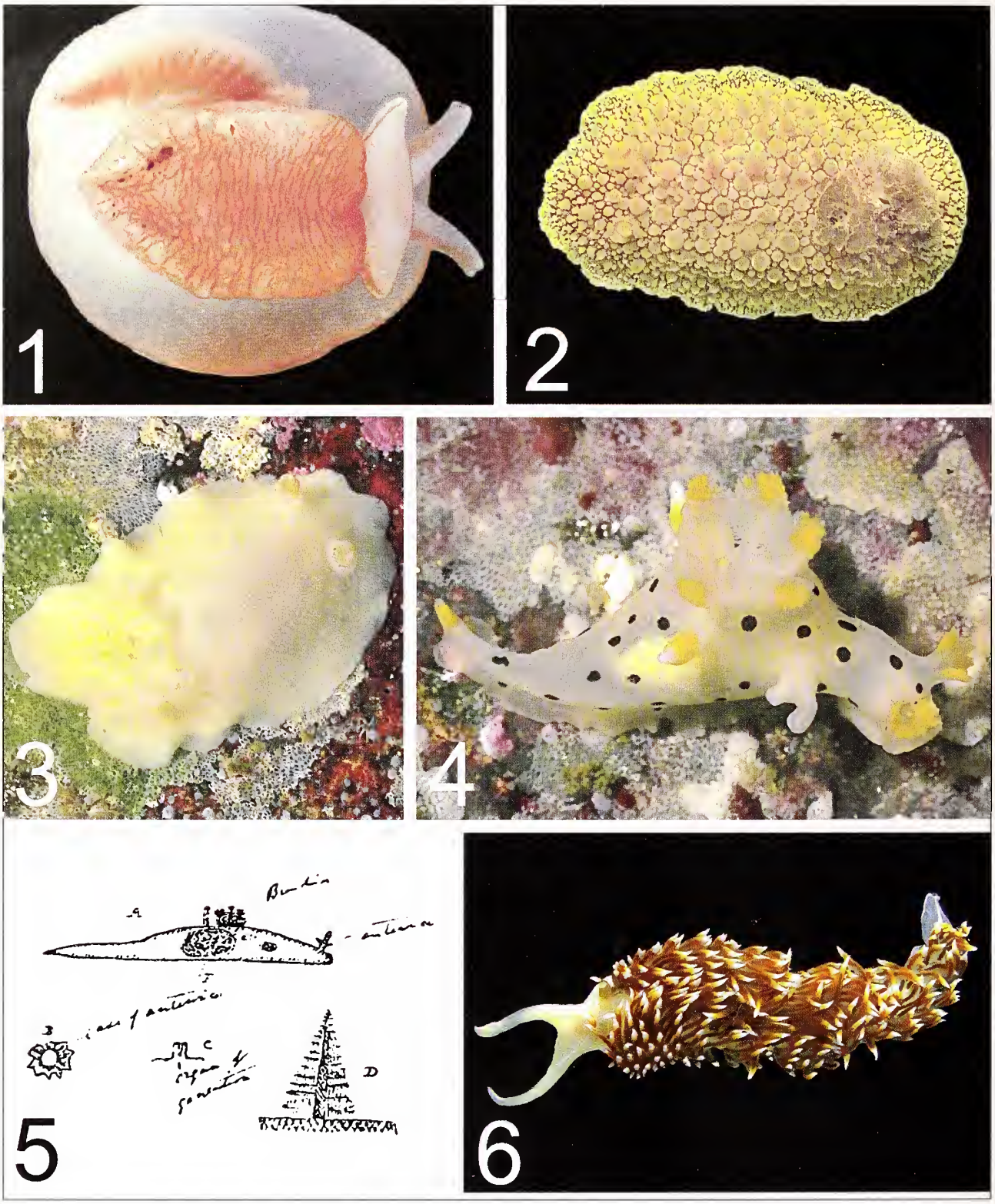

Figure 1: *Berthella platei*, living specimen (30 mm) from Lenca, ventral view.
Figure 2: *Anisodoris fontaini*, living specimen (55 mm) from the Bahía de Coliumo
Figure 3: *Anisodoris punctuolata*, living specimen (40 mm) from the Bahía de Coliumo (from SCHRÖDL, 1996: pl. III, fig. 20).
Figure 4: *Thecacera darwini*, living specimen (25 mm) from the Bahía de Coliumo (from SCHRÖDL, 1996: pl. V, fig. 33).
Figure 5: *Thecacera darwini*, DARWIN's original illustration (pl. 16, fig. 1; from KEYNES, in press, modified). Note the whole specimen in lateral view ("A"), the rhinophoral sheaths in view from above ("B"), a schematic drawing of the everted genital ducts ("C"), and a sketchy drawing of a single gill ("D").
Figure 6: *Phidiana lottini*, living specimen (60 mm) from the Bahía de Coliumo (from SCHRÖDL, 1996: pl. VII, fig. 41).

"Zoology Notes" (KEYNES, in press). Text in parenthesis within these citations are comments of the author. Some museum material of opisthobranchs collected during the "Beagle" was traced in the Cambridge University Museum of Zoology: only an *Aplysia* specimen and a specimen of *Bulla nitidula* from St. Jago, Cape Verde Islands are still in the collection (PREECE, pers. com.)

SYSTEMATICS

Incertae sedis

"Gasteropterus", "Port Famine" (Puerto Hambre, Magellan Strait), June 1834, roots of kelp, CD Page 264, species No. 996.

Remarks: The "straw-yellow" specimen was briefly described by DARWIN as having a mantle with sinuous edge and far surpassing the foot (mantle length 3.8 cm, width 2.8 cm). "Inferior antennae connected for 3/4 of length by a membrane" may either refer to a cephalaspidean head shield with projecting corners, or, more likely, to a pleurobranch oral veil with projecting oral tentacles. "Superior antennae" are "slightly winged", "branchiae" and viscera are " of rather a dark tint". No shell was mentioned. If truely a member of the genus *Gastropteron* Kosse, 1813, this would be the first and only record of Gastropteridae from temperate South American waters. However, the presence of two pairs of "antennae" makes this identification doubtful. On the other hand, no pleurobranch (or any other shell-less opisthobranch species with a mantle being much wider than the foot) with a sinuous mantle edge is known from the Magellanic region so far.

Notaspidea
Pleurobranchidae Fèrrusac, 1828
Genus *Berthella* Blainville, 1825

Berthella platei (Bergh, 1898).
(Figure 1)

"Pleurobranchus (crossed out) Sigaretus", east end of Beagle Channel, February 1834, at 3 m depth, roots of "Fucus Giganticus" (giant kelp), CD Page 217, Species No. 861.

REMARKS

DARWIN's description alone does not allow a more detailed identification other than the family Pleurobranchidae. However, according to a recent revision (SCHRÖDL, 1999) there is only one pleurobranchid species known from the Pacific part of the Magellanic region and from the southern Patagonian shelf, *Berthella platei* (Bergh, 1898). Therefore, it is highly probable that DARWIN first examined *B. platei*, 60 years before L. PLATE collected this species and gave it to BERGH (1898) for species description. Characterizing the invertebrate fauna around Chiloé Island in general terms, DARWIN (page 242) mentioned "Pleurobranchus" to be common.

Nudibranchia
Doridoidea
Discodorididae Bergh, 1891
Genus *Anisodoris* Bergh, 1898

Anisodoris fontaini (d'Orbigny, 1837)
(Figure 2)

"Doris", "Island of Caylen" (Queilén on Chiloé Island or Cailin Island, near Chiloé?), December 1834, "common under large stones", CD Page 284, Species No. 1091.

REMARKS

The "Doris" from Caylen differs from *Anisodoris punctuolata* (d'Orbigny, 1837) in its "egg-yellow" colouration and having "rounded" tubercles "of two sizes". In fact, there is only a single large, yellow Magellanic dorid species with two-sized, rounded tubercles, the common *A. fontaini*. All the externally similar species, *Anisodoris tessellata* Bergh, 1898, *Neodoris carvi* Marcus, 1959, *Neodoris erinacea* Marcus, 1959, and *Archidoris incerta* Bergh, 1898, were shown to be junior synonyms of *A. fontaini* recently (MUNIAÍN *et al.*, 1991; SCHRÖDL, 1997c, 2000a).

Anisodoris punctuolata (d'Orbigny, 1837)
(Figure 3)

"Doris", East Falkland Islands, 7 March 1833, 7 specimens, body dimensions 8.3 cm length: 3.8 cm width, CD Page 151.

REMARKS

This flattened, oval-shaped dorid with broad mantle externally resembles a group of similar, uniformly white or yellowish cryptobranch doridoideans, i.e. *Gargamella immaculata* Bergh, 1894, *Austrodoris kerguelenensis* (Bergh, 1884) and *Anisodoris punctuolata*. Only the latter two species reach the large body size of "3 1/4 inches" mentioned by DARWIN. Dense, minute notal tubercles ("surface... thickly studded with minute cylindrical papillae") only occur in *A. punctuolata*. Very interesting are DARWIN's detailed observations on the spawn (CD Page 151) describing egg-ribbons up to 20 inches long with no less than 600 000 eggs. Spawn of most Magellanic nudibranch species was studied by the author (unpublished data): only one large-sized, uniformly white or yellowish coloured Magellanic species with minute tubercles has been observed to produce such an enormous egg-ribbon, the common *Anisodoris punctuolata* (d'Orbigny, 1837).

?Discodorididae sp.

"Doris" (larger species), Cerro Tres Montes, Chonos Archipelago, December 1834, at 4 m depth, CD Page 292, Species No. 1108.

REMARKS

DARWIN (p. 292) suspected the "larger" (no dimension)

dorid being "pale yellow, with irregular brown spots" to be conspecific with the "Doris" (= *A. punctuolata*) from East Falkland Islands. Since no body dimensions are given, *Diaulula hispida* (d'Orbigny, 1837) (see SCHRÖDL, 2000b) could have been meant as well: its characteristic undulating ridge on the notum may be poorly developed and difficult to detect in individuals smaller than 3-4 cm (own observations).

?Platydoridae Bergh, 1891
cf. *Gargamella immaculata* Bergh, 1894

"Doris" (smaller species), Cerro Tres Montes, Chonos Archipelago, December 1834, at 4 m depth, 1.8 cm body length, CD Page 292, Species No. 1108.

REMARKS

The "smaller, bright yellow" specimen from C. Tres Montes might be *Gargamella immaculata* Bergh, 1894 (see SCHRÖDL, 1996, 1997a) having uniform colouration and "ten, small, delicate, brush-like" gills, but the description is too incomplete to be sure.

Doridoidea: Phanerobranchia: Polyceridae Alder & Hancock, 1845
Genus *Thecacera* Fleming, 1828
Thecacera darwini Pruvot-Fol, 1950
(Figures 4,5)

"Nudibranch", Cerro Tres Montes, Chonos Archipelago, December 1834, at 4 m depth, body length 2.5 cm when "extended", CD Pages 291- 292, pl. 16, fig.1; Species No. 1106.

REMARKS

This "nudibranch" from C. Tres Montes was exceptionally well characterized by DARWIN's external description: "...body very narrow, mantle not surpassing the foot, tail very much and abruptly pointed,....No labial (oral) tentacula, ...antennae (rhinophores) at their bases are enclosed in a case; which on the 2/3 of its exterior margin expands out into a saucer (rhinophoral sheath), the edges of which are intended with about 8 points, ...the branchiae are seated in very middle of the back; consist of five trees...placed in circle...A little posteriorly to the branchiae and a little exteriorly to them, there are two cylindrical, obtusely ended, tentacula-like organs rather longer than branchiae... Body white, singularly transparent: scattered over whole surface there are circular and oblong regular marks...color dark brown... The saucer-like case of tentacula: the branchiae, excepting the very tips: and central broad band in the two posterior cylindrical organs (top and base white): and narrow margin at very extremity of tail, bright orange. Hence very pretty animal". An interesting morphological detail is indicated in plate 16, fig. 1 (see Fig. 5): both the distal portions of male and female genital ducts are everted in dead specimens. These genital ducts are also everted by living specimens ready for copulation (own observation). In aquaria, *T. darwini* is able to float upside down on the water surface, confirming DARWIN's observation. In contrast to DARWIN's assumption "can probably swim well", *T. darwini* has never been observed swimming in natural surrounding or in laboratory. DARWIN correctly recognized this polycerid species as being "allied, especially in habits, to the molluscous one (hereby being identified as *Polycera* sp.) of Rio (CD p. 46). There can be no more doubt that DARWIN's Chilean polycerid specimens belong to *Thecacera darwini* Pruvot-Fol, 1950, which was described from preserved material from the Museé Nationale d'Histoire Naturelle Paris without knowing DARWIN's description in detail. Other polycerids from Magellanic waters, *Polycera marplatensis* Franceschi, 1928, and *P. priva* Marcus, 1959, clearly differ in colouration and body shape (for redescriptions see SCHRÖDL, 1996; MUNIAÍN & ORTEA, 1998).

Aeolidoidea
Facelinidae Bergh, 1890
Genus *Phidiana* Gray, 1850
Phidiana lottini (Lesson, 1831)
(Figure 6)

"Cavolina", Chiloé, December 1834, "under stones", 3.8 cm body length (crawling), CD Page 257, Species No. 1091.

REMARKS

The "Cavolina" from Caylen (CD p. 284) is not a pteropod Thecosomata as suggested by its misleading name, but an aeolidoidean nudibranch. The "general color crimson & brownish purple R. Mouth and under side finer rose color. Branchiae (cerata) composed of conical fillets, basal parts leaden colored, arranged in numerous transverse rows on each side of back...Anterior and inferior tentacula (oral tentacles) placed far apart..., very long, tapering, pointed, tipped with white" allow little doubt that DARWIN found *Phidiana lottini* (Lesson, 1831). This species is common along the coasts of southern Chile to Peru and was previously known under its junior synonym *Phidiana inca* (d'Orbigny, 1837). DARWIN also described the rhinophores as the "posterior and superior tentacula" being "blunt and much shorter, placed between (the latter word crossed out) behind some of the first rows of branchiae", while beginning not anterior to the level of the rhinophores in *P. lottini*. However, *Aeolidia papillosa* var. *serotina* Bergh, 1873, the only southern Chilean species with ceratal rows beginning anterior of the rhinophores, clearly differs in colouration, so that DARWIN's first observation that the rhinophores are "placed between" the first cerata appears to be correct.

DISCUSSION

In summary, DARWIN collected one notaspidean, at least four (probably six) different nudibranch species, and a dubi-

ous opisthobranch species from Magellanic waters but no museum material remains. More than 175 years after the "Beagle" cruise, however, every current researcher must be astonished at the detailed examination and description of some of his specimens, although without establishing and naming new species. He combined morphological and biological information which, in the case of *Anisodoris punctuolata*, now enabled species identification. DARWIN even dissected specimens of *A. punctuolata*, thus providing some anatomical information, long time before other researchers recognized the importance of anatomical studies in opisthobranchs; all this in the consideration that DARWIN was not a molluscan specialist and only had rudimentary literature at his disposal (see KEYNES, 1997). The most striking example for DARWIN's accuracy is his detailed and unambiguous morphological and biological description of *Thecacera darwini*. This beautiful nudibranch species was named in DARWIN's honour by PRUVOT-FOL (1950), however, without knowing his early description in detail. With the present study, *T. darwini* is confirmed as definitely referring to DARWIN's species.

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